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Vol. 70, No. 3 July 1972

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Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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SCIENTIFIC EDITOR'S NOTE

This issue of the *Fishery Bulletin* is dedicated to Dr. Oscar Elton Sette who, until his retirement, was a senior scientist of the National Marine Fisheries Service and its predecessors. All of the contributors owe a debt of gratitude to Dr. Sette and have used the following pages to express their appreciation to him. However, the number of contributors to this issue is only a small fraction of the fishery scientists who have been significantly affected by knowing this fine man. It is for all of them that I say thank you, Dr. Sette.

Reuben Lasker

Oscar Elton Sette.

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OSCAR ELTON SETTE

I cannot imagine a more pleasant task than this—to write a prefatory statement for the Oscar Elton Sette issue of the *Fishery Bulletin*. It is also a most difficult task, for one must choose one's words with care lest he become maudlin and guilty of oversell on the one hand, or reserved to the point of disparagement on the other.

I do not propose to list Elton Sette's accomplishments and honors (these are recited elsewhere), but only to comment on and quote others on certain aspects of his career that may help us attain perspective.

It was not long ago that I left the 18th meeting of the Eastern Pacific Oceanic Conference (EPOC), before its conclusion and before Elton Sette stepped down as Chairman of that eminently successful "non-organization." He had conceived the idea and served as the sole (always temporary) Chairman through the history of this informal, nonstructured conference, at which attendees speak freely, representing only themselves in their capacity as experts and not necessarily speaking the party line of their parent organizations. The success of EPOC in developing ideas and plans, in bringing about coordinated efforts over a wide spectrum of scientific disciplines, is a measure of the way the man works: low key, low pressure, high performance.

Over a decade ago, on January 16, 1961, he received the Department of the Interior's highest honor, the Distinguished Service Award. In his citation, Secretary of the Interior Fred A. Seaton said this:

> Dr. Sette is an internationally recognized leader in marine science, highly respected by his contemporaries in University, State, and Federal Service. His ability has speeded progress in the knowledge of the sea and its resources, and reflected prestige and credit upon the Bureau of Commercial Fisheries and the Department. Since joining the Bureau of Fisheries, a predecessor agency of the Fish and Wildlife Service and Bureau of Commercial Fisheries, on January 8, 1924, he has made outstanding contributions not only as a scientist, but as an organizer of investigations, eminent administrator, and an unusually successful teacher . . .
>
> He has always placed special importance on the training of scientists under his supervision and has devoted much time and effort to their development. These efforts have had an important influence upon fishery science in the United States and Canada, as attested by the numbers of his former employees who now hold leading positions in the profession.

That such things should be said of a man who has already made a significant impact for the good upon society is appropriate and expected. But I find two earlier statements of perhaps greater interest for they show that his attributes were recognized at the very earliest stage of his career.

Some 50 years ago (fifty!), W. F. Thompson was Director of the fledgling California State Fisheries Laboratory. He employed a young college student, O. E. Sette, apparently in 1919, and wrote this for the January 1921 issue of "California Fish and Game":

> Mr. O. E. Sette, who has been with the [California] Commission for more than a year, has also returned to his college work, having left for Stanford on September 1 [1920] . . . . The Commission is fortunate in being able to retain the interest and services of Mr. Sette, whose work has been of high value.

Then, in January 1924:

> The fisheries investigation work of the Commission appears to be a training school for government fisheries men, for several who have been mainstays have been tempted to other positions by higher salaries . . . now comes word that O. E. Sette has accepted a prominent position with the United States Bureau of Fisheries . . . . Nor is it an easy matter to find the right kind of scientifically trained men to fill these vacated positions. Although discouraging, those in charge are planning to carry on by acquiring the best material available to fill these positions.

His worth was obviously apparent at a most tender age to no less stringent a taskmaster than W. F. Thompson.

From a personal standpoint, I knew him by repute from my first delvings into fisheries

literature as a student. My first real contact with his work came when, as a very junior biologist at that same State Fisheries Laboratory, I was given the task of recompiling some length frequencies of Pacific mackerel, which were measured in units called "settes." The man I knew of, the measurement not. It turned out he established the half centimeter as appropriate for mackerel during his days at the laboratory. The unit later became known as the sette, and the term was used for over a decade until the half centimeter finally fell from grace, being deemed insufficiently precise. I first met him some years after my encounter with the sette and found that the good reports that preceded him were excelled only by the man himself.

So with this issue we honor as best we can someone who has earned the respect and admiration of those fortunate enough to have crossed his path during his long and most honorable career. He is in the truest sense a gentle man.

Philip M. Roedel

OSCAR ELTON SETTE: FISHERY BIOLOGIST

PATRICIA POWELL[1]

The twentieth century marked a turning point in the development and advancement of many scientific disciplines. Pioneer leaders at this time turned to research, focusing their explorations on ways and means of increasing man's knowledge about himself and of the world in which he lives. Within a lifetime, these leaders made an impact on society that changed social and economic structures and continues to do so. Oscar Elton Sette, fishery biologist, is one of this select group. His contributions to marine fisheries and his astute administration of fishery research places him among the foremost of his contemporaries. He pioneered research in two oceans. He was among the first to expand the concept of fishery biology to include other disciplines, and succeeded in integrating this science with those of oceanography and meteorology, elevating it to a major status and advancing its economic importance worldwide.

A midwesterner by birth, Sette spent his early years in an environment quite different from that which was to hold his attention for more than fifty years. His parents, Martin and Louise, lived in Clyman, Wisconsin, where his father owned a retail lumber business. On March 29, 1900, their fourth child Oscar Elton Sette was born. The Settes also had two daughters and another son. A few years after Elton's birth, the family moved to a small town of Juneau, Wisconsin, for business reasons.

It was in Juneau that Elton, as he preferred to be called, learned reading, writing, and arithmatic; and developed a lasting love of nature, together with a scientific curiosity concerning all living things. He says his great love was for "natural history studies," particularly those of butterflies. At a very early age, he collected butterflies which he classified, and had a truly remarkable collection of Lepidoptera by the time he finished high school. He has continued to collect these insects throughout his life, and when work pressures were great in later years, claims this hobby afforded the release he needed to prevent ulcers. He also collected stamps.

Martin Sette always wanted to retire on a lemon ranch, and with this in mind bought five acres near Chula Vista, California. Later he bought another five acres. When some of his investments went "sour," he decided to live on the ranch and grow lemons. The family moved to southern California in 1910. During some lean years that followed, Elton's mother, who firmly believed in the principle of "waste not, want not," instilled a sense of frugality in her children. This quality, which Mr. Webster defines as "careful management of resources," has been reflected in her son's thinking down the years.

Between the ages ten and sixteen, Elton was kept busy with school activities and the pursuit of his hobbies. He graduated from the eighth grade when he was twelve, then attended high school in National City, California, for four years. He was an outstanding student and planned to enter college, expecting to get a degree from the University of California at Berkeley in Entomology. However, fate, by the name of Elmer Higgins, stepped into the picture in 1916. Owing to a chain of circumstances in which Dr. Higgins played a part, Elton's plans for college did not materialize. Instead of becoming a "bug-hunter," his interest was diverted from butterflies to fisheries. His first encounter with this gentleman came during his senior year in high school. The following is a quote from an anectodal review of Elton Sette's career as written by Elmer Higgins:

> "My first contact with Elton Sette occurred in September, 1916, when a trim, compact, boy in knickers and shirt filed into my chemistry classroom and laboratory with a couple dozen other students in National City (Calif.) High School. I was a 'freshman' science

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teacher on my first job after receiving my secondary school teacher's certificate and in my zeal I must have borne down rather heavily on my students, but most of them took it and seemed to like it.

"Came the end of the first 'advisory period' and I reported three or four students to the Principal as failing to make satisfactory grades. Among them was Elton Sette. The next day, the Principal came to me with a worried expression to ask what was the trouble, explaining that Elton was starting his senior year and everyone expected him to graduate with honors. I agreed that Elton was learning chemistry (witness the very good grades he earned in the frequent little written quizzes), but he seldom was prepared to recite on the day's assigned section in the textbook and, moreover, his laboratory notebook was quite incomplete.

"Elton apparently had acquired the habit of listening intently in class to the recitations and discussions of his more diligent classmates, sorting and storing the pertinent facts in his retentive and discerning mind, and instantly recalling them to write an excellent examination paper. The Principal gravely agreed to speak to Elton. Elton's performance immediately improved, and he went on to graduate as the Valedictorian of his class."

Almost two years passed before Sette encountered Elmer Higgins again. He had been attending San Diego Junior College, with definite plans to enter the University of California in the fall of 1918. Then, one day as he was walking down a street in San Diego, they happened to meet. Higgins invited Elton to accompany him on an exploratory trawling trip. When Elton saw what came up in the nets, he was fascinated. He knew right then he wanted to become a fishery biologist. Elmer Higgins was now working at the California State Fisheries Laboratory in San Pedro as a scientific assistant. Dr. Wm. F. Thompson, Director of the Laboratory and in charge of fishery investigations in southern California, was especially interested in the albacore fishery, and needed observations of landings from San Diego. He asked Higgins if he knew of any former student who could be recruited for summer work. Higgins immediately wrote Sette who agreed to check the canneries for albacore landings. So, Elton Sette, through the chance intervention of Elmer Higgins, began his career working with fisheries at 18.

He did not enroll at the University in Berkeley that fall as planned. Instead, he joined other young men his age and served in the U.S. Army. World War I was in the final stages. Upon his discharge in 1919, he joined the staff of the State Fisheries Laboratory.

A definite program of scientific investigation concerning the sardine was inaugurated in 1920 by Dr. Thompson. The increasing commercial importance of this fishery made it necessary to learn about sardine habits and determine the effects of fishing on the resource. Elton Sette was assigned to this investigation from the beginning. He was sent to Monterey, the center of the great sardine canning industry.

In his first report, Sette wrote "Hopkins Marine Station courteously granted the Fish and Game Commission use of quarters and facilities." Other accounts described his office as "a daydreamer's paradise, punctuated with bird watching, and girl watching, in the picturesque cove below." In spite of distractions, he states the investigation was carried on "energetically." His first article was published in *California Fish and Game* in October 1920. In this publication he described the Monterey fishery, his work, and expressed a prophetic interest in the yearly fluctuations in abundance and sizes of the fish as well as concern for the fishery unless "intelligent conservation measures" were adopted. This early interest in the underlying causes of fluctuations in pelagic fish abundance and what can be done to prevent the depletion of these resources has remained with him throughout the years.

In September 1920, he took a leave of absence to attend Stanford University to finish college. His two years there were rich ones, for under David Starr Jordan's guidance Stanford was the center of fisheries research on the west coast. Many Stanford graduates became outstanding leaders in various aspects of fishery science. It was a great peer group, and lifelong associations were formed in the inspiring, informal gatherings where ichthyology and research problems were discussed. But it was not all work or talk. Sette found time to play tennis and collect butterflies on Jasper Ridge. He graduated with a Bachelor of Arts in Zoology in June 1922.

After graduation Sette continued his work with the State Fisheries Laboratory, as a scien-

tific assistant, alternating between Monterey during the sardine fishing season and the San Pedro Laboratory to work on tuna investigations in other months. His first major contribution to fishery literature reported his analysis of the sardine data he collected at Monterey as well as various sampling systems he used. It was submitted for publication in April 1924.

Sette used an increasing amount of statistical analysis in his study of the sardine fishery. This came to the attention of U.S. Commissioner of Fisheries, Henry O'Malley, who persuaded him to move to Washington, D.C. and join the U.S. Bureau of Fisheries as Chief of the Division of Fishery Industries. He held this position from 1924 to 1928. Managing this division included supervising research in fishery technology, particularly the canning and preservation of fishery products, and the distribution of technological and production information to the public. He also was given the special task of improving the Federal Government's system of collecting and publishing statistics. During this time, his own publications were confined to annual statistical and economic reports of United States fisheries, and articles concerning commercial fisheries for Bureau publications or trade journals.

The year 1924 was one of change and growth for Elton. Living in the capital city was quite different from that of the west coast, the new job was entirely different from that of his previous experience, and he relinquished his bachelorhood. He had met and fallen in love with Elizabeth G. Jackson whom he married December 20 of that year.

The new job was stimulating, but Sette never lost his interest in fishery biology, nor in the challenge to manage large fluctuating fish resources. So he began on his own to study the Atlantic mackerel which had yielded widely different catches over a period of years. Once again Elmer Higgins entered his life. Higgins had been appointed Chief of the Division of Scientific Inquiry, U.S. Bureau of Fisheries, and was stationed in Washington, D.C. He encouraged Elton in his mackerel research and offered him a position in his Division as full-time investigator. Sette decided to accept in 1928. Meanwhile, increased appropriations from Congress made it possible to establish regional research teams to investigate important fisheries, or types of fisheries. Because of his experience and personal competence, Sette was made Chief of the North Atlantic Fishery Investigations, a position he held until 1937.

He established headquarters at the Museum of Comparative Zoology at Harvard University, and recruited a handpicked staff to study the life histories of marine fish important to the New England coast as well as the effect of fishing on their abundance. At the same time, Sette concentrated his own attention on the Atlantic mackerel. The published results of this study represent a significant contribution to fisheries research and is a classic in the literature. During the summer months he acted as Director of the Bureau's Fisheries Station at Woods Hole. He also found time to continue his studies, at the graduate level, and obtained his Master's Degree in Biology at Harvard in 1930. Of Sette and his staff, Dr. Higgins wrote:

> "..... (they) worked in a sort of happy symbiosis with the staff of the M.C.Z., the Faculty, and graduate students, many of whom were employed by the Bureau on temporary appointments. Thus, the haddock investigations began, the cod investigations wound up, the weakfish studies of the mid-Atlantic coast were extended, and oceanographic examination of the Gulf of Maine was brought to a virtual completion. All of these efforts resulted in a number of significant papers."

One of Sette's most endearing qualities to those who worked under him, especially students and young men starting their careers in marine science, was his ability to meet with them and discuss work at their level, to draw them out, and inspire them to put forth their best effort. One such student was Dr. Daniel Merriman, present Director of Sears Foundation for Marine Research. He worked part time for Sette in the summer of 1930 while he was taking an invertebrate course at the Marine Biological Laboratory. He has written:

> "I cannot imagine how I got the job unless it was through the good offices of Dr. Henry Bigelow, a close family friend. My record at Harvard had nothing

to commend me, and the only thing I can think of was a teen-age association with Dr. A. G. Huntsman at St. Andrews, New Brunswick. In all events, I sorted mackerel eggs and larvae to a fare-thee-well. But the point is, the work never became tedious under Sette's watchful eye. I thoroughly enjoyed it and him, and in vicarious fashion I learned a lot; it was by far my most rewarding summer to date. Bigelow, Huntsman and Sette: three men who nudged an aimless youngster into a happy and rewarding career. I shall always be eternally grateful to O. E. S. for his patience and his stimulus."

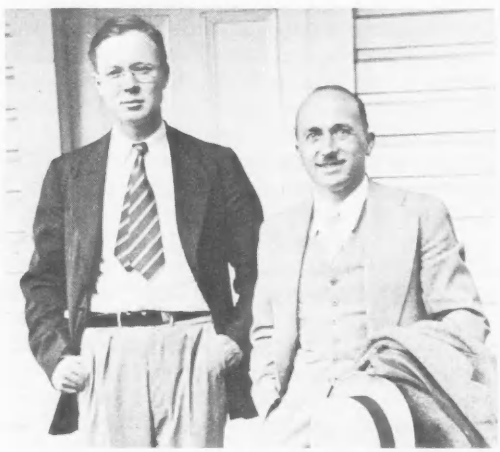
Forty years later another young man, just starting his career, has written:

"During the summer of 1965 I worked in Dr. Sette's Lab as a seasonal aid type. I learned more in 2½ months working with Dr. Sette and his staff than I did in the 4 years at the College of Fisheries. The people who work with Dr. Sette work as a team. Each individual has his own talents and Dr. Sette augments these talents. Somehow through empathy and compassion he frees you to your limitations and helps you to work beyond your own ability. Each specialist from secretary to oceanographer is fully aware of the entire effort.—there are far too few Dr. Settes."

So wrote Richard A. Winnor, Associate Marine Biologist, California Department of Fish and Game, in 1972.

Sette's pleasant days at Harvard and Woods Hole lasted nine years, in which time knowledge of fishery resources on the Atlantic coast was advanced significantly. Meanwhile a crisis was developing on the Pacific coast. The sardine fishery, which gave indications of mushrooming back in the early twenties, had expanded beyond all expectations within two decades. From 1916 through 1939, the catch more than doubled each six years, and reached its maximum in 1936 with a billion and a half pounds landed. State fishery biologists were concerned and warned against overfishing. Nationally, concern for the nation's food supply was developing, and demands were being made for a better scientific basis of fishery management. Since the state was unable to control the fishing industry through legislation, a Congressional investigation was made. Because of his proven ability to manage a fishery resource, his past experiences with the sardine fishery, and his contacts with the industry, Sette was sent to California by Congressional mandate, to head a sardine research program inaugurated by the Bureau, a position of great responsibility. He was made Chief of the new South Pacific Fisheries Investigations, with headquarters on the Stanford campus. His duty statement proclaimed "he was to direct and perform research on the nature and causes of fluctuations in pelagic fish populations." This fooled no one. N. B. Scofield, Chief of the State Bureau of Marine Fisheries, resented federal intervention in California fisheries investigations and openly remarked the best thing Sette could do was to pack his bags and go back to Washington. The industry also wanted no federal intervention and regarded Sette's operations with suspicion. However, his mild and friendly personality had won him many friends among the industry in the early twenties. Those who did not know him had a great respect for his work and his personal honesty, as did the biologists with the Division of Fish and Game, many of whom were old friends. His marked success in handling this delicate situation is an example of Sette's personal tact and diplomacy.

For several years strong disagreements existed between the industry and the Fish and Game Commission. Canners were critical of techniques used by the State's biologists and of



John L. Hart, Fisheries Research Board of Canada, and O. E. Sette.

their evaluation of the sardine data. As a result, the San Francisco Sardine Association and the California Sardine Products Institute engaged Sette as a paid consultant from 1942-1947. Their respect for his judgement was so great they followed his advice without question when he said he could not conscientiously recommend industry requests for additional tonnage. Julian Burnette, a prominent business man who was active in industry affairs during that time, commented that Sette never spoke unless he had something to say, and when he did, people listened.

Marine fishery research was practically eliminated during World War II owing to a manpower shortage and the use of fishing vessels for the war effort. Between 1943 and 1945, Sette served as Area Coordinator of Fisheries for California. He applied strict control on all plants and vessels that were operating in the California fisheries. He assigned boats to different plants and shifted them around so all plants would be in operation and no waste would occur. Controlling a fiercely competitive industry was an especially difficult assignment. His success was rewarded by a meritorious promotion in 1944, in his capacity as Chief of the South Pacific Fisheries Investigations where he remained until 1949.

The post-war years witnessed a boom in commercial fishing and ushered in a period of expansion in fishery research. The search for new sources of protein to meet the demands of a growing population, as well as the economic aspects of harvesting large pelagic fish stocks attracted monied interests internationally. The need to discuss mutual problems and exchange information between scientists engaged in fishery research in other countries resulted in a series of international meetings. Sette attended several of these as an official representative for the United States.

Meanwhile the sardine fishery in California experienced an alarming decline. Concern over the depletion of this resource gave rise to public demand for answers from fishery biologists to explain what caused the fluctuation of this once great fishery. The answer to this problem already had challenged Sette's thinking for a quarter of a century. It was obvious that such answers could be sought only through the cooperation of various agencies working together on a multidisciplined research program. In 1947 the California State Legislature established the industry-financed Marine Research Committee. The Committee, consisting largely of industry members, and with Sette as its scientific advisor, inaugurated the California Cooperative Sardine Research Program which became the California Cooperative Oceanic Fisheries Investigations, or CalCOFI. Five agencies participated at the Federal, State, and University levels. Sette's fine hand was evident throughout the planning stages. He was largely instrumental in integrating the disciplines of fishery biology with those of oceanography and meteorology as this program developed. His personal contributions to the program and his participation in symposia at annual meetings were significant.

The fishing pressure exerted on tuna stocks throughout the Pacific ocean prompted the federal government to initiate tuna research in the mid-Pacific in 1949. Money was appropriated to build a large, well equipped laboratory adjacent to the University of Hawaii campus and to purchase two vessels designed for this specific program. Sette was appointed Director of the new Honolulu Laboratory and made Chief of the Pacific Oceanic Fishery Investigations, or POFI as it was called. Here, under his leadership, an exceptional research staff was assembled. The team, consisting of fisheries biologists, oceanographers, and meteorologists, jointly launched another pioneer program to study environmental phenomena and their relationship to oceanic fishes. In their studies of tuna resources along the equator, a subsurface current was detected. The name of this current honors its discoverer, Townsend Cromwell. The masses of other data published provided a great source of new information about the central Pacific Ocean.

While in Hawaii, Sette was an enthusiastic gardener and he took great pride in his flowers, fruits, and vegetables. He recycled matter for his own compost long before recycling became a popular conservation measure. His zeal for composting caused a family crisis. Apparently his wife, Elizabeth, thought the compost was

Staff of Pacific Oceanic Fishery Investigations, Honolulu, Hawaii. Left to right: Walter M. Bosworth, Administrative Assistant; Keith Elliott, Statistician; Harold T. Smither, Administrative Officer; Donald L. McKernan, Assistant Director; O. E. Sette, Director; Harry B. Hinkle, Operations Officer; Albert K. Akana, Marine Operations Superintendent.

(Photograph courtesy of *National Fisherman*)

responsible for breeding centipedes, which reach considerable size in Hawaii. Often they found their way into the house where Mrs. Sette received several bites. These she was quick to blame on her husband and his compost.

He was also an avid tennis player, and a good one. While at POFI he encouraged and organized tennis tournaments at the Lab. When a tournament was held, it was mandatory that a player show up for the matches, no matter how severe the hangover.

Representatives of the tuna industry did not think Hawaii was the right location for the Bureau's tuna investigations. They wanted this research centered in California near the tuna canneries and the fishing fleet. Charles Carry, Director of the Tuna Research Foundation and spokesman for the industry, often gave Sette a bad time about this and other matters. In this connection, Carry tells about an incident that happened in Santiago, Chile, where he and Sette were attending an international fisheries meeting in 1955. In all of Carry's frequent trips to the Honolulu laboratory, he had never seen Elton take a drink, and knew it was because he suffered from stomach ulcers. But in Santiago, Elton drank with the rest of the group. Carry asked why. Sette replied, "I have learned not to take myself too seriously, nor you, Charlie."

Each new assignment in Sette's life was an expansion of his original interest. For five years at POFI, his primary responsibilities were to direct research and exploration on potential fishery resources. Then in 1955, a new program called Ocean Research came off the Bureau's drawing board, and once more Sette was called to pioneer a new direction in fishery research. He was returned to the Stanford campus as Chief of Ocean Research and director of another new laboratory broadly chartered to examine all available data concerning the oceans and relate these to the abundance and distribution of fish. He set about the herculean task of analyzing masses of sea surface temperature data, weather observations, and all known information concerning fish availability. With the help of a small but highly skilled team of biologists, oceanographers, and meteorologists, an atlas containing 168 monthly mean sea surface temperature charts for the Pacific Ocean north of latitude 20°, covering the years 1949-1962, was published. This remarkable man still found time to complete

his graduate work, receiving his Doctorate in Biology from Stanford University in 1957; to give lectures at the University; to continue collecting butterflies on Jasper Ridge as he had done in his student days; and to publish on a species of Lepidoptera from central California.

Sette always has been a firm believer in the value of informal meetings. He was instrumental in organizing the Pacific Tuna Conferences; he helped structure and actively participated in the CalCOFI Conferences as he had in the Sardine Meetings from their beginning in 1920. He chaired, or was a committee member of, numerous planning and steering committees throughout the years. EPOC was a natural outgrowth of his experience working with groups.

In 1954 at a meeting of the Oceanography Fisheries Meteorology Committee, Sette proposed that various groups engaged in related investigations in the eastern Pacific join together to coordinate the planning and execution of work at sea, and to exchange information on research program results. His proposal was acted upon in the Committee's 1955 meeting, and EPOC, or the Eastern Pacific Oceanic Conference, was born. EPOC held its first meeting in 1956 with Elton Sette as chairman and Joseph L. Reid, Jr., as Secretary. For fifteen dedicated years both men served EPOC and the entire ocean science community. They made possible a forum for discussion of oceanographic research and provided a medium by which the farflung investigations of diverse academic and governmental agencies could be coordinated.

Dr. Sette's administration of international oceanographic investigations to study stocks of fishes that recognize no political boundaries, brought him in close contact with scientists of other countries who also were interested in these pelagic resources. He attended many international meetings to discuss common problems. He was an official United States delegate to the Indo-Pacific Fisheries Council in Singapore in 1949 and to the International Technical Conference on the Living Resources of the Sea in Rome in 1955. He acted as Advisor to the U.S. Delegation at a Fisheries Conference, Santiago, Chile, in 1955, and at the Law of the Sea Conference, Geneva, 1958. He participated in numerous other meetings as a committee member, council correspondent, or by presenting a paper.

He has served as a consultant on oceanography to the Director of the Bureau of Commercial Fisheries and as special consultant to the Atomic Energy Commission. He was a member of the Ocean Resources Panel of the National Academy of Sciences and is an advisor to the University of California, Institute of Marine Sciences.

Numerous professional and technical societies have his support as an active member, including Phi Beta Kappa and Sigma Xi. He is a founding member of the American Institute of Fishery Research Biologists, and a Fellow of the American Association for the Advancement of Science. Others include: American Fisheries Society; American Institute of Biological Sciences; American Society of Ichthyologists and Herpetologists; American Society of Limnology and Oceanography; American Wildlife Society; Biometric Society; California Academy of Sciences; Oceanographic Society of the Pacific; and, Western Society of Naturalists.

For outstanding service to the Federal Government, Oscar E. Sette was presented the U.S. Department of Interior's gold medal award for distinguished service on January 16, 1961. The medal and citation delivered by Assistant Secretary Leffler before an audience of several hundred reads in part as follows:

> ". . . . In recognition of his important contributions to the scientific program of the Bureau of Commercial Fisheries and his eminent career in Government, the Department of the Interior bestows upon Dr. Sette its highest honor, the Distinguished Service Award.
>
> FRED A. SEATON
> Secretary of the Interior."

It seems more than coincidental that sitting on the stage beside Dr. Sette that day was Dr. Elmer Higgins, who also received the Distinguished Service Award for outstanding achievement.

Dr. Sette's accomplishments are legion. It would be difficult to select any one as the most outstanding. He modestly sums up what he considers to be his major achievements in two succinct statements. These are: contributions to knowledge regarding pelagic sea fish and fisheries; and, the planning, organization, and

Opening a cocoanut, Hawaii.

directing through their formative years, the four research programs he administered for forty-two years. Equally significant, and perhaps greater, is the sustaining influence he exerted throughout the years as Chairman of EPOC and a guiding member of CalCOFI and other such research groups. Here, his uncanny ability to foresee a problem situation and sidestep the issue before it became a crisis was especially valuable. Also important are the untold hours of service rendered government agencies, the scientific community, the industry, and others as a technical advisor, special consultant, official delegate, leader, and friend. Over and above all is the remarkable contribution of the man himself through his personal warmth, his unusual ability to inspire, his patience and perception as a teacher, his gift of enthusiasm for his own work and that of others, and most of all, his genuine interest in and love of people.

There is an impressive list of publications to Sette's credit, in spite of his time-consuming administrative responsibilities. Several have been mentioned above. Other important papers include: *Estimation of the abundance of the eggs and larvae of the Pacific pilchard off southern California during 1940 and 1941* (Sette and Ahlstrom, 1948); *Considerations of midocean fish production as related to oceanic circulatory systems* (1955); *Problems in fish population fluctuations* (1961); *Ocean environment and fish distribution and abundance* (1966); and *A perspective of a multi-species fishery* (1969).

Sette also found the time to keep up with current literature in his own fields as well as that of others which intrigued his scholarly or scientific interests. His own library is extensive, and he, personally, has indexed most of the material pertaining to ocean sciences. Sette's memory is retentive, and when asked, he can call to mind papers on specific subjects, although the article may have been written years ago.

When asked his choice of a place to live, he chose California, with its long coastline and mild sunny climate. He and Mrs. Sette make their home in Los Altos where they have resided for many years. They are a devoted family, and enjoy having their only daughter, Josephine Helene Barnes, and her family live nearby in San Jose. The Robert F. Barnes have two young sons, ages four and seven, who are a source of great pleasure to their grandparents.

Needless to say, the Settes' garden is a place of beauty, as well as a practical source of food. Planned with the precision of a research program, the yard is planted in rotation to produce a continuous supply of fresh vegetables and flowers from early spring throughout the fall months; and, they enjoy a succession of fruit in season from the many varieties he has cultivated or skillfully grafted to parent trees. The flowers attract the butterflies Sette loves, and have given rise to a backyard investigation, in his spare time, of a subtropical species *Agraulis vanillae*, which appeared early in 1960, enticed by the passion flower plants growing in the garden. Hoping to keep the small population alive during the winter months, Sette started growing passion flowers in the lathe house to protect the eggs and larvae from unaccustomed cold. He began to study the fluctuation of their populations, observing the time of emergence and the relationship to warmth and sunshine. This correlation to warm, sunny spring days fostered an interest in amateur meteorology, which has developed into another hobby. Daily he observes the humidity and the barometric pressures and follows the passing lows and highs with interest. This keen sense of awareness of his surroundings is a delightful part of his personality.

On paper, in compliance with government regulations, Dr. Oscar Elton Sette, Senior Scientist, "retired" in March 1970. He was immediately rehired as an "annuitant" which is permissible in Federal service, to continue his research and prepare for publication a backlog of data. The Ocean Research program was concluded in June 1970, and the laboratory at Stanford was closed. He is presently attached to the Tiburon Laboratory, National Marine Fisheries Service, in charge of the Ocean Ecology unit, headquartered in Menlo Park. With the assistance of a secretary-librarian his keen mind is busily engaged with many of the unsolved problems facing fishery researchers. He is working on several papers, one of which is the analysis of the Alaska herring fishery. His duty statement on his appointment papers fill two typed pages, single spaced. They end with . . . . . "a high degree of confidence is placed on his productivity, competence, and judgement. He is recognized as a top authority and distinguished scientist in his field." It is interesting to note that his present title is: Fishery Biologist (Research).

For more than half a century Dr. Oscar Elton Sette, fishery biologist, leader of leaders, has continued to pioneer the development and advancement of fishery research as an outstanding scientist, a great humanitarian, and a warm and sincere friend to all of his associates.

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RESEARCH AND THE FISHERIES SERVICE'S SECOND 100 YEARS

PHILIP M. ROEDEL[1]

A year ago, in 1971, we celebrated the one hundredth year of a Federal fishery service. This was an occasion, depending upon the individual, for self-congratulation, a tabulation of a century of successes, wonderment that so many could accomplish so little in so long, and on the part of a number of us serious thought and study of where the first century had brought us and whence we might wish the second to lead us. What can we learn from the past; how should we change our ways if we are to cope adequately with problems as we see them today and foresee they will be tomorrow?

The first century had its moments of great success, its moments of failure, and we can expect the same in our second, hoping and planning that there will be more of the former and fewer of the latter. This first century began with the era of descriptive ichthyology, with fisheries science as we know it today growing from these beginnings. We can follow the development of the science from one essentially zoological—and a limited range of zoology at that—to one encompassing all aspects of biology, particularly physiology and genetics, and going beyond the biological sciences to oceanography, mathematics, and statistical analysis in our attempts to understand and predict fluctuations in abundance. Rather late in the first century we find food science entering as a partner in fisheries research. Only recently has there been an acceptance, unfortunately still given grudgingly in some circles, of economic, social, and legal research as legitimate fisheries tools.

The first century, until its last decade or two, was one in which the pace was leisurely. There was time for thoroughgoing analysis, for programs that satisfied the scientist's legitimate and proper desire to have a full understanding of the system he was studying before making pronouncements on or recommendations concerning its status or management.

To be sure, it was concern over the status of certain stocks that led to the establishment of the Federal fishery service in 1871, and of, for example, the California State Fisheries Laboratory in 1917, and the International Fisheries (now Halibut) Commission in 1924. The collapse of the Pacific sardine fishery in the 1940's gave warning that the pace of research might be too slow, that scientists might be called upon for recommendations based on—to them—insufficient evidence, that fisheries science could ill-afford internecine warfare, and that a new breed of man, the skilled biopolitician, was desperately needed if the findings of the scientists were to be translated into effective laws in time to do any good for an overfished stock.

It was also forced upon our attention in the remaining two decades of this first century that other nations had indeed developed a new breed of fishermen, one that has changed all the rules of the game.

The tremendous fishing power of the distant-water fleets, their worldwide mobility, and their capability for pulse fishing finally brought home to us toward the close of the first century the fact that fisheries now could be explored, developed, exploited, overexploited, and left to their fate in far less time than traditional methods of stock assessment could give an estimate of optimal yield. We found also that existing political and institutional arrangements were not capable of responding to these new pressures.

To cope with this we must turn to rapid assessment techniques, reliance on data that once would have seemed pitifully inadequate, to "quick

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and dirty" surveys that are an anathema to the purist but vital in what we see as the real world today.

This last decade—the 1960's—has also brought forth most clearly that resolution of environmental problems is critical if we are to have any fish left for us—or other nations—to fish or if we are to pursue aquaculture as a significant means of food production. This area of research, tackling as it does matters of environmental quality, of the impact of environmental degradation on living organisms and in turn on man the consumer, and of what can be done about it, must be one of primary concern to us as we move into the second century.

Another set of factors is influencing our course of action most strongly. Fishery scientists and administrators, particularly the latter, have always been cognizant of them but have not as a general rule faced up to them. These factors deal with the common property nature of fishery resources and the economic and legal problems associated therewith. Quite obviously, the finest biological research in the world is of little avail if proposals for utilization or management based on its results cannot be implemented. On the one hand, we have serious problems of allocation of available stocks among political and social entities; on the other we have a series of regulatory systems that tends generally to perpetuate economic inefficiencies and to lead to overcapitalization.

The biologist cannot cope properly with these serious and highly complex problems, though too often he was forced to try in recent decades because the fisheries field simply did not have sufficient professional talent in such areas as law and economics associated with it.

The need for economic research has for some years been recognized as essential, and work in this area is going on apace in both the Federal fisheries service and in several universities. Economics is not, however, the only "new" discipline involved in the fisheries problems we now face. Legal research, particularly in the field of international and constitutional law, is obviously pertinent. It is equally critical as we become more and more concerned with domestic allocation and control of fisheries and the allocation of resources among competing users of the environment. Are estuaries for fish, for industry, for marinas—or for all of them, perhaps plus something else? Is a given species for the sportsman, for the commercial fisherman—or for both of them, perhaps plus someone else? Here we move into a generally unplowed field and that falls partly at least within the purview of still another professional—the sociologist.

In Century I, fisheries science moved from ichthyology into fisheries biology, added other biological disciplines such as physiology and genetics, accepted mathematics and statistics as integral to success, incorporated physical oceanography, engineering, and physics into the fold, touched on meteorology, became deeply involved with biochemistry and food science, and opened the door to economists and lawyers. The future will hold a greater role for the social sciences and the legal profession, but it will remain the fisheries scientist (whatever he may be—some mix of biologist, ecologist, oceanographer, and mathematician) who will provide the requisite scientific data with which other disciplines can interact to provide the final synthesis upon which the administrator can base his decision.

Research in the Fisheries Service at present falls into three major categories: (i) biological, ecological, and oceanographic research of the sort traditionally conducted by fisheries biologists, including fisheries oceanography, population dynamics, inshore ecology, studies of contaminants and disease, aquaculture, a smattering of gear technology and instrumentation, and so on; (ii) fishery technology and marketing research; and (iii) economic research, this of necessity growing to encompass matters of a social, institutional, or legal nature.

All of this is being carried on so that we may fulfill our mission as we see it: to promote the wise use of living marine resources for their aesthetic, economic, and recreational value to the American people. Our basic objectives within the framework of that mission are to understand and protect living marine resources and the environmental quality essential for their existence, and to devise rational schemes for resource allocation and development.

We are thus striving for many things in our research program. If they are to be of maximum value, they must produce results that will assist us in our attempts to keep as many fishery management options open to the Nation as possible.

We need, then, reasonably precise measures of abundance of the living marine resources, and of their response to varying types and degrees of fishing pressure—foreign, domestic, sport, and commercial. We need to know of their distribution in time and space, of the impact on them of environmental changes whether induced by man or by nature. We must cope with a wide variety of technological problems, some of them requiring short-term responses. And economic, social, and legal research must concern itself with a wide variety of programs, ranging from rather basic economic analyses of each fishery, to developing means for overcoming such problems as property rights and split jurisdiction, and determining the economic and social benefits of fisheries resources to the Nation.

It is within this framework and toward resolution of these problems that our programs and efforts are being redirected as the Fisheries Service enters its second hundred years.

DEVELOPMENT OF THE LANTERNFISH, *SCOPELOPSIS MULTIPUNCTATUS* BRAUER 1906, WITH A DISCUSSION OF ITS PHYLOGENETIC POSITION IN THE FAMILY MYCTOPHIDAE AND ITS ROLE IN A PROPOSED MECHANISM FOR THE EVOLUTION OF PHOTOPHORE PATTERNS IN LANTERNFISHES

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ABSTRACT

The larval and transformation stages of the unusual myctophid, *Scopelopsis multipunctatus* Brauer, are described. A character that the larvae of *Scopelopsis* share with a number of other genera in the Lampanyctinae is the sequential development of three or more pairs of early forming photophores. The sequence of development of early forming photophores is shown to be an especially useful character in revealing phylogenetic affinities when used in conjunction with other larval characters, such as body shape and pigment pattern. From our study of the development of *Scopelopsis*, a possible mechanism for the evolution of photophore patterns within the family Myctophidae is presented.

Brauer (1906), in his elegant report on the fishes collected during the German Deep-Sea Expedition of 1898-99, described for the first time a remarkable lanternfish, for which he established the genus *Scopelopsis*. His single specimen, a newly transformed juvenile, was unique in having the head and body studded with minute light organs, all of approximately the same size. All other lanternfish known to him were characterized by a specific pattern of photophores on the head and on the ventral and lateral regions of the body. These he grouped into the single genus *Myctophum*, under which he recognized four subgenera: *Myctophum, Diaphus, Lampanyctus*, and *Lampadena*. These two genera, along with *Neoscopelus*, a genus with an undifferentiated pattern of ventral photophores, and five other genera were included in the family Scopelidae.

Regan (1911) modified drastically this taxonomic arrangement by distributing Brauer's eight genera of scopelids into a scheme of three suborders. He placed the family Myctophidae within one of these suborders and included within it seven genera: *Scopelopsis*, *Neoscopelus*, *Scopelengys* (a genus related to *Neoscopelus* but lacking photophores), and the four subgenera of Brauer raised to generic rank. Parr (1928) further differentiated the family Myctophidae to include three subfamilies: Scopelengini for *Scopelengys*, Neoscopelini for *Neoscopelus*, and *Scopelopsis*, and Myctophini for *Myctophum*, *Lampanyctus*, *Diaphus*, and *Lampadena*.

Tåning (1932) noted that in a number of well-preserved specimens of *Scopelopsis*, certain photophores were larger and better developed than others, and that the scales covering these organs were equipped with the same lens-like modification typical of other members of Parr's Myctophini. He observed further that these larger photophores formed a pattern that corresponded with the kinds of photophore patterns found in the Myctophini and concluded, accordingly, that *Scopelopsis* belonged with *Myctophum*, *Lampanyctus*, and relatives in the subfamily Myctophini.

Fraser-Brunner (1949) reduced the number of subfamilies in the Myctophidae to two: The Neoscopelinae, to include *Neoscopelus*, *Scopelengys*, and *Solivomer*, and the Myctophinae, to in-

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clude *Scopelopsis* and 20 other genera. He provided the first substantial description of the photophore pattern of *Scopelopsis* and, in his illustration, differentiated the more conspicuous "primary" photophores from the minute "secondary" organs. Further, he recognized two major evolutionary lineages among these 21 genera and placed *Scopelopsis* among the group which included *Lampanyctus* and its relatives.

Authors since Smith (1949) have afforded full family status to the neoscopelines, separating the three genera from the Myctophidae. Recently, Paxton (1968) reviewed the osteology of the Myctophidae and constructed a higher classification to reflect generic relationships within the family. His views have been stimulative and complementary to our studies of larval myctophids (Moser and Ahlstrom, 1970). Our recent discovery of the larvae of *Scopelopsis* has served to crystallize our views of relationships within that part of the family which contains *Lampanyctus* and its allies. These ideas, based chiefly on larval morphology and sequence of photophore development, are set forth herein, following the description of *Scopelopsis* larvae.

MATERIALS AND METHODS

The developmental series of *Scopelopsis* used in this study was obtained chiefly from the R.R.S. *Discovery* plankton collections, housed at the British Museum (Natural History). A total of 29 specimens was taken off South Africa at stations 412, 413, 416, 418, 419, and 438 in August-September 1930. An additional five larvae were found on station 2352, occupied off South Africa in July 1938. A single transforming specimen came from station 2280 of the U.S. Antarctic Project ship *Eltanin*. Although adult specimens of *Scopelopsis* were obtained on EASTROPAC surveys, larvae were not taken.

A series of 25 specimens, from smallest larva to juveniles, was measured according to the method described in Moser and Ahlstrom (1970), to produce the table of morphometrics essential for description of the changes in body proportions. These specimens also were used for describing the development of the melanophore pattern and of photophores. A second series of 11 larvae was cleared with KOH and stained with Alizarin Red-S; a table of meristics was constructed from counts made on these specimens.

For purposes of discussion we have included information and illustrations of nine genera related to *Scopelopsis*. These specimens and data, accumulated over an extended period of time, have come largely from the plankton collections of the California Cooperative Oceanic Fisheries Investigations, the NORPAC Expedition, the EASTROPAC Expedition, and the Danish Oceanographic Expedition, in addition to the two sources mentioned above. Where specimens from these and other sources are illustrated, appropriate station data are included in the caption accompanying the figure.

DESCRIPTION OF DEVELOPMENT OF *SCOPELOPSIS MULTIPUNCTATUS*

(Figures 1-3)

LITERATURE

Regan (1916) described the species *Lampanyctus longipinnis* from a 15-mm larval specimen. Judging from the fin counts given in the description and from the somewhat illegible drawing, the specimen was a larva of *Scopelopsis multipunctatus*.

MORPHOLOGY

Larvae of *Scopelopsis* are moderately slender. Body depth at the pectoral fin base is 18-19% of the body length in larvae undergoing notochord flexion and is 20-24% (mean of 22%) in later larval stages and transforming specimens (Table 1). The gut is of moderate length in specimens undergoing notochord flexion; snout-anus length is 44-45% of body length. The gut is conical in these specimens and gradually arches posteriad to the short terminal section. Snout-anus distance increases slightly in later larval and transforming specimens, which have a snout-anus length of 50-54% (mean of 52%) of body length. In these, the gut is covered by trunk musculature.

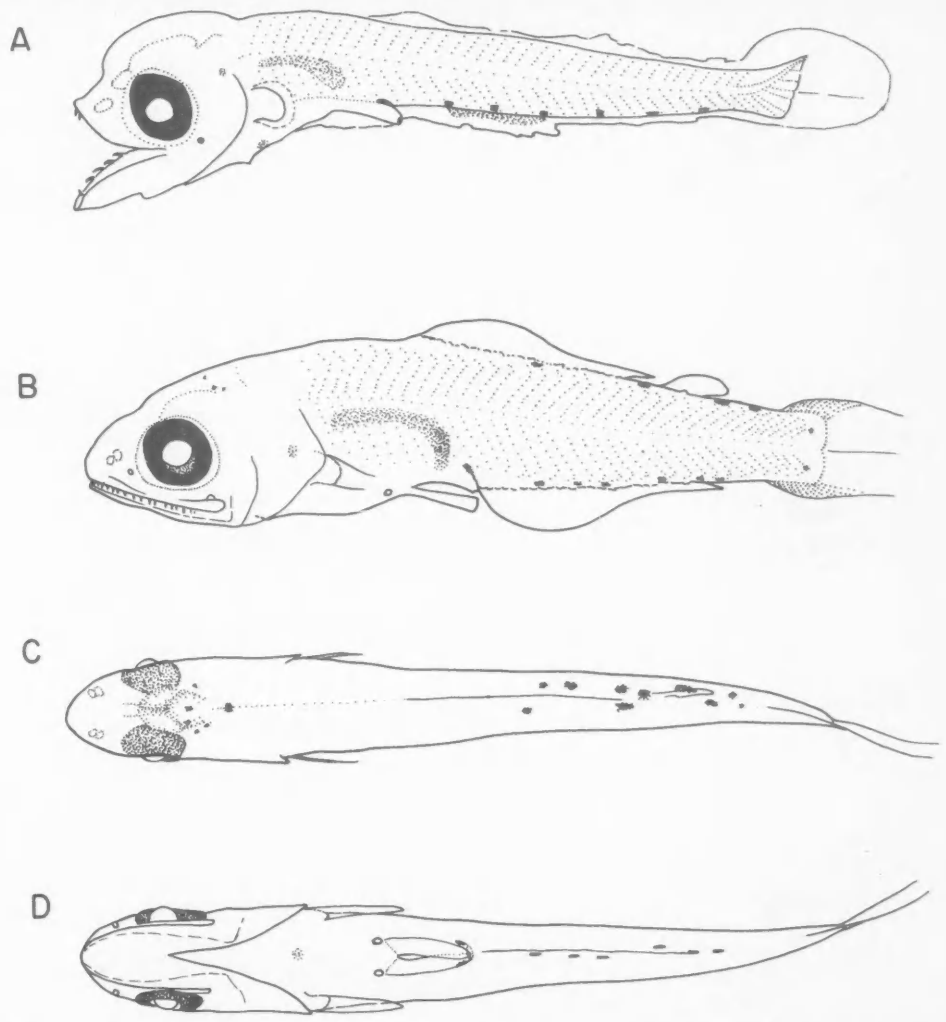

FIGURE 1.—Developmental stages of *Scopelopsis multipunctatus* Brauer.—A, 5.4-mm larva, R.R.S. *Discovery* Station 2352; B, 11.3-mm larva, R.R.S. *Discovery* Station 2352; C, 11.3-mm larva, dorsal view; D, 11.3-mm larva, ventral view.

The head is moderately large, its length being 24-28% (mean of 27%) of the body length for the larval series. The dorsal profile of the snout is concave in our smallest specimen (5.4 mm), but is straight in a 6.2-mm larva, and becomes distinctively bulbous in later larvae and in transforming specimens. The eyes are large in *Scopelopsis* larvae, but undergo a slight diminution, relative to head size, with progressive larval development. Eye length measured vertically is 38% of the head length in the smallest larva, but decreases to 35% in a 6.2-mm larva. This dimension averages 30% of the head length in larvae which have completed notochord flexion,

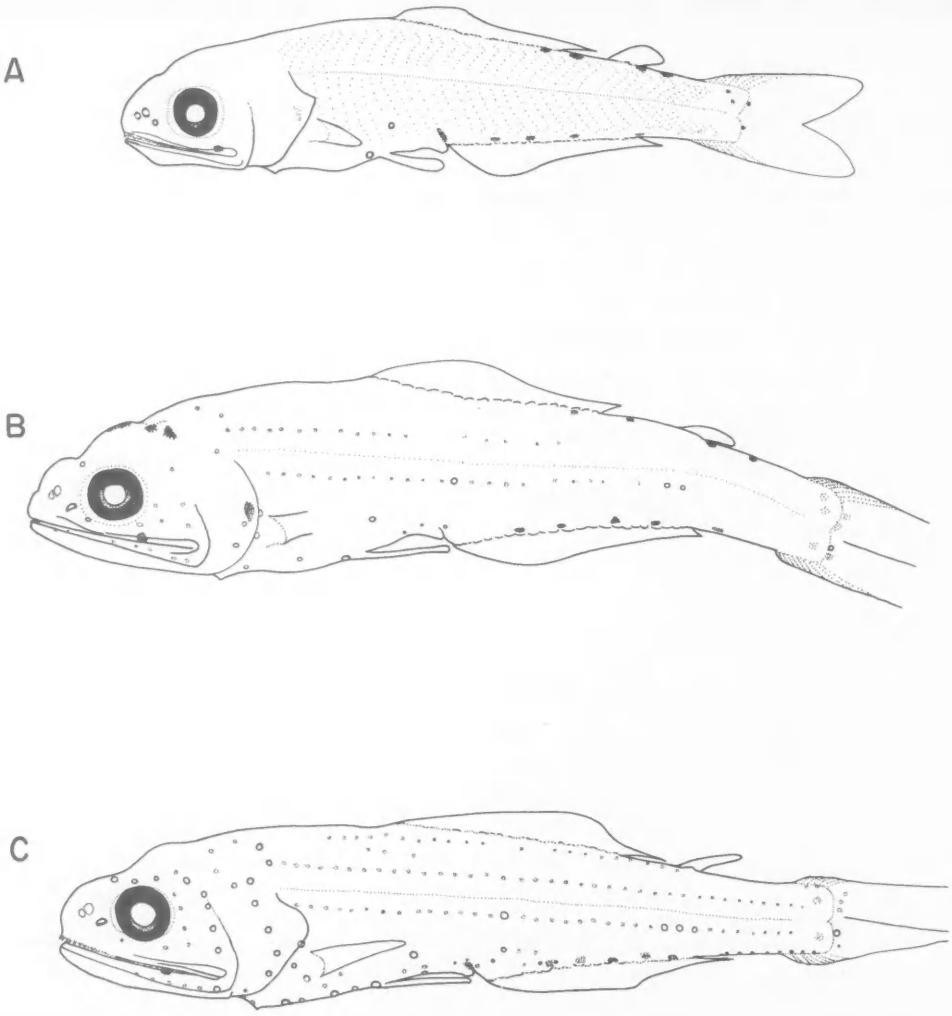

FIGURE 2.—Developmental stages of *Scopelopsis multipunctatus* Brauer.—A, 13.4-mm larva, R.R.S. *Discovery* Station 412; B, 17.6-mm transformation stage, R.R.S. *Discovery* Station 2280; C, 16.7-mm transformation stage, R.R.S. *Discovery* Station, 419.

but this is reduced to an average of 25% in transforming specimens and to 22% in a newly transformed juvenile. The eyes are round or nearly so in *Scopelopsis*; eye width, measured horizontally, averages 92% of eye length for the larval series. In the 17.4-mm juvenile, the horizontal measurement is slightly greater than the vertical. Choroid tissue is absent from the ventral surface of the eye. The initial lateral teeth of the lower jaw are characteristically curved anteriad. Later, the more typical dentary teeth form anterior to the curved teeth; the latter occupy the posterior half of each dentary in larger larvae.

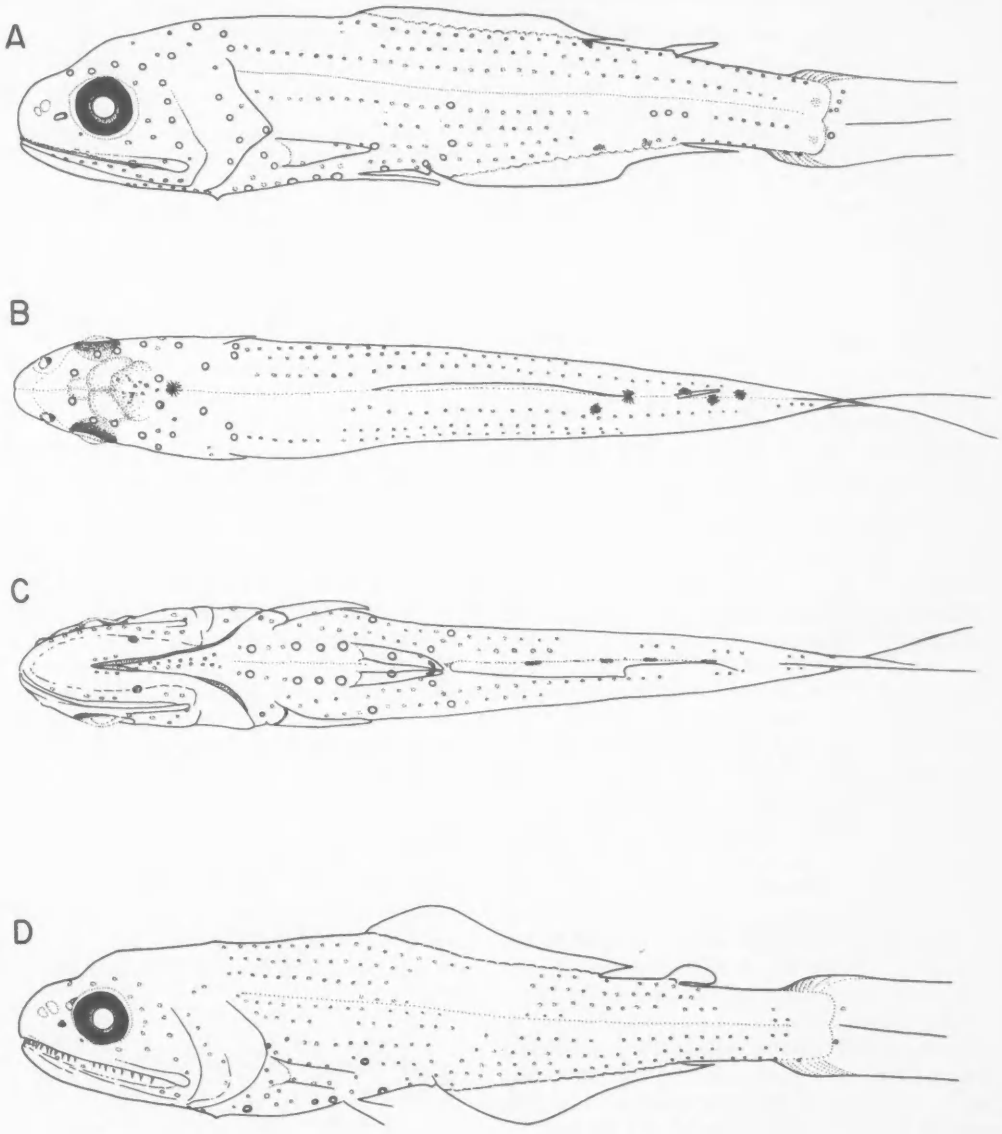

FIGURE 3.—Developmental stages of *Scopelopsis multipunctatus* Brauer.—A, 17.5-mm transformation stage, R.R.S. *Discovery* Station 419; B, 17.5-mm transformation stage, dorsal view; C, 17.5-mm transformation stage, ventral view; D, 17.4-mm juvenile, R.R.S. *Discovery* Station 412.

TABLE 1.—Measurements (mm) of larvae of *Scopelopsis multipunctatus*. (Specimens below dashed line have completed notochord flexion.)

Body length	Snout to anus	Head length	Head width	Inter-orbital width	Body depth at base of pectoral fin	Eye length	Eye width	Snout to origin of anal fin	Snout to origin of dorsal fin	Snout to origin of pelvic fin
5.4	2.4	1.3	0.76	0.46	1.0	0.50	0.43	2.8	--	--
6.2	2.8	1.7	0.87	0.58	1.1	0.59	0.52	3.1	2.8	2.4
10.8	5.4	2.8	1.4	1.2	2.2	0.87	0.81	5.4	4.6	4.1
11.3	5.8	3.2	1.5	1.3	2.5	1.0	0.95	5.8	5.0	4.6
12.2	6.4	3.2	1.6	1.3	2.7	1.0	0.90	6.4	5.2	4.8
12.3	6.3	3.2	1.6	1.3	2.6	0.94	0.86	6.3	5.2	4.8
12.4	6.5	3.3	1.7	1.4	2.6	1.0	1.0	6.5	5.4	5.0
12.8	7.1	3.3	1.8	1.4	3.0	1.1	1.0	7.1	5.6	5.4
13.0	6.8	3.4	1.7	1.4	2.8	1.0	0.95	6.8	5.7	5.2
13.1	7.1	3.4	1.8	1.5	3.1	1.0	0.91	7.1	5.8	5.3
13.2	6.7	3.2	1.8	1.5	2.8	0.97	0.83	6.8	5.5	5.2
13.4	7.0	3.6	2.1	1.5	3.1	1.0	0.87	7.0	5.8	5.3
13.5	6.9	3.5	1.8	1.4	2.8	1.1	0.91	6.9	5.8	5.2
13.8	7.4	3.7	1.8	1.4	2.8	1.1	1.0	7.4	6.1	5.5
13.9	6.9	3.5	1.8	1.5	2.9	1.0	0.92	6.9	5.9	5.3
14.2	7.4	3.8	2.0	1.5	3.2	1.0	0.95	7.4	6.2	5.7
14.3	7.4	3.7	1.8	1.4	3.1	1.0	0.95	7.4	6.2	5.5
14.6	7.4	3.8	1.8	1.7	3.2	1.1	1.0	7.4	6.2	5.4
14.9	7.8	4.2	2.0	1.7	3.2	--	--	7.8	--	6.1
15.2	8.2	4.2	1.9	1.7	3.3	--	--	8.2	7.0	6.2
15.5	8.2	4.4	2.0	1.7	3.4	--	--	8.2	7.0	6.2
[1]16.7	8.8	4.6	2.3	1.9	3.8	1.2	1.1	8.8	7.0	6.7
[1]17.5	8.8	4.8	2.5	1.8	3.6	1.2	1.2	8.8	7.2	6.9
[1]17.7	8.8	4.8	--	--	3.8	1.2	1.2	--	7.4	6.7
[2]17.4	9.0	4.9	2.4	1.9	3.7	1.1	1.2	9.0	7.2	6.9

[1] Transformation stage.
[2] Juvenile.

FIN DEVELOPMENT

Our smallest specimen (5.4 mm) is undergoing flexion of the tip of the notochord and already has the adult complement of 10 superior and 9 inferior principal caudal rays (Table 2). In the next smallest larva (6.2 mm), also undergoing notochord flexion, a single procurrent ray is forming in the superior and inferior series. The adult complement of 10-11 superior and 10-12 inferior procurrent rays is present in larvae 13.0 mm and larger.

The pectoral fins are represented by their inconspicuous bases in the 5.4- and 6.2-mm specimens; the fins themselves are membranous, with no ossified rays. Description of the gradual acquisition of ossified rays described for pectoral fins of other species (Moser and Ahlstrom, 1970) is precluded by the gap in our series of *Scopelopsis*. Larvae 10.8 mm and larger have the adult complement of 10-11 rays in each fin.

The bases of the dorsal and anal fins are beginning to form on the 5.4- and 6.2-mm larvae, but no rays are ossifying. Larvae 10.8 mm and larger have the adult complement of 21-23 dorsal and 23-25 anal rays.

The pelvic fin buds are present in the 6.2-mm larva, and larvae 10.8 mm and larger have the adult number of 8 rays in each fin. The adipose fin is beginning to develop at 6.2 mm and is well formed by 10.8 mm.

Gill rakers and vertebrae develop later than do the fins. Gill rakers are first apparent in the 10.8-mm larva and are added gradually. On the first arch, the full complement of 7-9 epibranchial rakers is achieved at 13.5 mm while, on the lower limb of the arch, the full complement of 15-17 rakers is present at 15.2 mm. A 10.8-mm larva already has 34 vertebral centra forming; the adult number of 37-40 vertebrae is present in larvae 12.2 mm and larger.

TABLE 2.—Meristic characters of cleared and stained larvae of *Scopelopsis multipunctatus*.

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper left limb	Lower right limb			Left	Right	
5.4	10	9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6.2	10	9	1	1	--	--	--	--	--	1	--	--	--	--	--	--	--
10.8	10	9	9	10	8	8	11	11	4	3	4	12	24	23	8	8	34
12.2	10	9	9	10	9	9	10	10	4	3	6	12	24	22	8	8	39
13.0	10	9	10	11	10	10	10	11	4	3	6	14	23	21	8	8	38
13.5	10	9	11	12	9	9	10	10	4	3	7	14	24	22	8	8	39
13.9	10	9	10	12	9	9	11	11	4	3	7	14	25	23	8	8	39
14.3	10	9	11	12	9	10	11	11	4	3	7	14	24	22	8	8	38
15.2	10	9	11	11	10	10	11	12	4	3	8	16	24	22	8	8	39
15.7	10	9	9	11	10	10	11	10	4	3	8	15	23	22	8	8	39
17.6	10	9	10	12	10	10	10	11	4	3	8	16	24	23	8	8	39

PIGMENTATION

Scopelopsis larvae develop a distinct pattern of melanophores. The smallest larva in our series (5.4 mm) has a prominent median melanophore at the nape and a smaller melanophore embedded in the otic region at each side of the head. Another large melanophore is embedded at the ventral midline, just below the bases of the pectoral fins. An equally prominent melanophore lies above the gut, at the point where the free terminal section diverges from the body. An elliptical shield of melanophores lies above the developing gas bladder but is partially masked by the body wall musculature. A series of six evenly spaced melanophores is embedded along the ventral midline of the tail. All the melanophores that constitute this initial pattern remain throughout the larval period. The series at the ventral midline of the tail usually contains five or six melanophores in older larvae; specimens with fewer than three or more than eight were not found.

Another major area of pigmentation is visible in a 6.2-mm larva, which has two melanophores in the dorsal midline posterior to the adipose fin. In larger larvae this series extends anterior to the dorsal fin, with the usual condition being a series of three, four, or five melanophores on, or on either side of, the midline. An 11.3-mm larva has the maximum number of 10 melanophores in this series, with several of the melanophores positioned along the base of the dorsal fin.

Final additions to the melanophore pattern are in the head and caudal fin. In specimens 10.8 mm and larger, a melanophore is embedded anterior to the base of each pectoral fin, and specimens 11.3 mm and larger have one to several melanophores above the posterior region of the brain. Larvae 10.8 mm and larger have one to several melanophores embedded in the hypural region of the tail; these melanophores may lie over the superior hypurals, the inferior elements, or both. Similarly, in specimens 12.3 mm and larger, one to several melanophores may be found at the base of the caudal rays, either at the superior group, the inferior group, or both. Some specimens lack these caudal ray melanophores. A few larvae have an additional median melanophore at the junction of the hypural elements and the rays.

PHOTOPHORE DEVELOPMENT

A number of photophores develop in larvae of *Scopelopsis* in a prescribed sequence.[2] As in most other myctophids the Br_2 are the first to form. They are just visible in our smallest specimen (5.4 mm) and are well formed in a 10.8-mm specimen. The next to appear is the posteriormost PO pair which is just visible in the 10.8-mm larva but is well formed, although small, in

[2] For clarity, a diagram of the characteristic photophore groups of adult myctophids is shown in Figure 4.

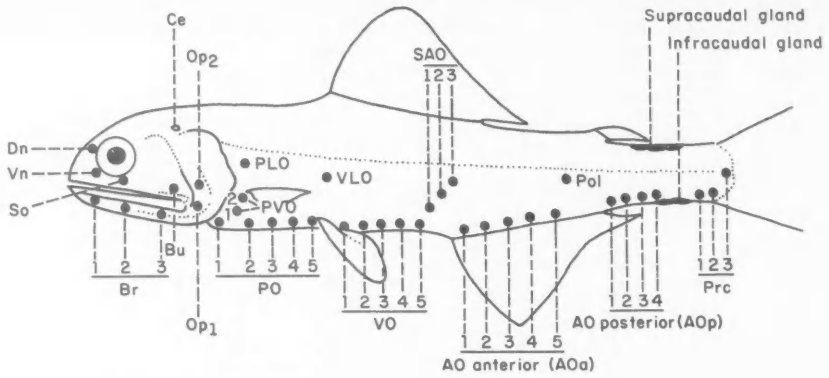

FIGURE 4.—Diagram of characteristic photophore groups of adult myctophids (modified from Nafpaktitis and Nafpaktitis, 1969 and Fraser-Brunner, 1949).

larger specimens in the series. The next to develop are the Vn; they appear anteroventral to the eye in the 11.3-mm larvae and become progressively cup-shaped as development proceeds. At the end of the larval period they are the largest photophores present. During transformation they begin to be overlain with tissue and bone so that they are difficult to see in juveniles and adults; this is doubtless why they have been overlooked by recent authors (Fraser-Brunner, 1949; Nafpaktitis and Nafpaktitis, 1969). The fourth pair of photophores to develop are the VLO; they first appear slightly posterior to, but well above, the bases of the pelvic fins in a 13.4-mm larva.

The four pairs of photophores described above are the only ones to develop until the larvae reach about 15-mm length. In a series of five larvae 14.9-15.7 mm long, a number of other photophores are beginning to appear. In the jaw region one is visible just below the terminus of each maxillary, and another is forming above and slightly anterior to the end of the maxillary. One or two others are developing in a line extending dorso-anteriad from the latter cheek organ. Dorsally on the head, a photophore is developing above the lateral margin of each olfactory lobe. In the PO series two pairs are evident, one slightly posterior to the juncture of the cleithra and another pair equidistant between this pair and the most posterior pair, described above. A VO pair is developing midway between the bases of the pelvic fins and the anus. Farther posterior on the body, the SAO_3 are developing as are the posteriormost Prc pair.

The photophore pattern is augmented further in the three remarkable transforming specimens illustrated in Figures 2 and 3, in which the adult pattern of photophores is clearly emerging. The three represent a developmental series of which the 17.6-mm specimen is the least advanced, followed by the progressively more advanced 16.7- and 17.5-mm specimens. In the 17.6-mm specimen the previously described photophore pattern on the head is augmented by several organs below and to the rear of the eye, by a line of organs along the lower jaw, and by several on the opercle. On the body a PLO and one PVO is present at the pectoral fin base, several organs are forming above the vent, and two POL are arranged horizontally above the end of the anal fin. In addition, two horizontal lines of photophores are beginning to appear, one above and one below the lateral line. The adult photophore arrangement of *Scopelopsis* is clearly manifest in the 16.7- and 17.5-mm specimens. Photophores are beginning to cover the head in a definite pattern; some of these are considerably larger and more defined than others. On the body the many regular rows of secondary organs are emerging, al-

though the following larger and more distinct primary photophores stand out on the 17.5-mm specimen: PO_{1-4}, $PVO_{1 \text{ and } 2}$, VLO, VO, SAO_{1-3}, POL_{1-3}, Prc.

In the 17.4-mm juvenile it is evident that the photophores on the body are on the posterior margin of each scale pocket, thus explaining their regular arrangement into horizontal rows. The specimen is partially skinned, but one can see that some body photophores remain decidedly larger than others (notably two of the PO, the VLO, and VO), while generally the distinction between primary and secondary organs is less marked. On the head, certain of the cheek photophores remain large and distinct and, additionally, the two-part Dn is now present as are the small anterior and posterior Br.

Opinion has been divided on whether or not the dichotomy of primary and secondary photophores, described above, is present in adult *Scopelopsis*. In his original description Brauer (1906) did not distinguish between primary and secondary organs. Tåning (1932) stated that some of the organs were larger than others and, moreover, made the important observation that the scales over these larger organs were equipped with a special lenslike modification typical of other myctophids. He noted that among the prominent photophores were a PLO, two PVO, a VLO, three SAO in a rather steep line, and two POL in a horizontal line. His statement, "... in fact we find all the different groups of organs which we have in all other species of the subfamily Myctophini, small, but larger than the very small organs scattered all over the body..." was unaccompanied by an illustration. Fraser-Brunner (1949) recognized that certain photophores were more highly developed than others and termed these primary organs in contrast to the less highly developed secondary organs. He gave the following formula: "PLO above, both PVO below base of pectoral. Five PO. Five VO. Three SAO in an oblique series. AO in two series. Two POL in horizontal series. Five or more Prc." His accompanying illustration shows the basic photophore pattern but is somewhat illegible, especially in the caudal region. Nafpaktitis and Nafpaktitis (1969) could not differentiate primary and secondary photophores in their material. Wisner (in press) employed a large series of excellently preserved specimens in his description of *Scopelopsis* and showed that the ability to differentiate primary from secondary photophores is dependent on the condition of the specimen. In specimens which had retained most of their scales he identified primary photophores as those with a lenslike modification of the overlying scale. His photophore formula and clear illustration corroborate the observations of Tåning (1932) and Fraser-Brunner (1949); further refinements include his observation of 7-10 anterior AO, 5-6 posterior AO, 4-6 Prc, 2 or 3 POL, and 3 prominent cheek photophores in a diagonal line anterior to the preopercle. Additionally he shows definitively the two-part Dn and the embedded Vn. The observations of Tåning (1932), Fraser-Brunner (1949), and Wisner (in press) along with the evidence presented herein demonstrate that certain of the multitudinous light organs of *Scopelopsis* are more highly developed than others and that these "primary organs" are arranged in a pattern that corresponds to the general pattern of other members of the family. Our observations on ontogenetic series largely confirm the arrangement of primary photophores postulated by these authors, but some of our findings suggest discrepancies that may only be clarified by further examination of undamaged adults. For example, we find only four well-developed PO and a single large VO in transforming specimens and in juveniles and adults available to us. This as well as the exact frequencies of AO and Prc series await elucidation by workers with large series of intact adults.

SYSTEMATIC RELATIONSHIPS

The efficacy of using the larval and transformation stages of lanternfishes to elucidate specific and supraspecific relationships has been clearly demonstrated (Pertseva-Ostroumova, 1964; Moser and Ahlstrom, 1970). We (Moser and Ahlstrom, 1970) showed that the genera of Myctophidae can be divided into two groups on the basis of larval eye shape—those with narrow elliptical eyes and those with round or nearly

round eyes. That these are phylogenetically natural groups is supported by Paxton (1968, 1972) who, on the basis of adult osteology and photophore arrangement, formally established the same two groups of genera as subfamilies. He grouped the 11 genera with narrow-eyed larvae into the subfamily Myctophinae and the 17 genera with round-eyed larvae into the subfamily Lampanyctinae. Further, in our paper we described the evolutionary lineages within the Myctophinae as evidenced by the structure of the larvae. Many of our conclusions agreed with those of Paxton (1968), derived from adult characters, but we differed ultimately with his distribution of the 11 myctophine genera into two tribes and with his derivation of the subfamily Lampanyctinae from an already highly evolved lineage of the subfamily Myctophinae. The larvae of the subfamily Lampanyctinae, although morphologically conservative compared with those of the Myctophinae, are useful, nonetheless, in revealing evolutionary lineages within the subfamily. The diversity of eye shape, so spectacular in the Myctophinae, is absent in the Lampanyctinae, but the eyes of many genera are distinctive because of their size, subtle but characteristic deviation from the basic rounded outline, or presence of a ventral crescent of choroid tissue. Likewise each genus of Lampanyctinae has a characteristic body shape, although the subfamily lacks the diversity of body form, so dramatic in the Myctophinae. The peculiar modifications of the paired fins, common among the larvae of Myctophinae, are generally absent in the Lampanyctinae; only in the lampanyctine genera *Lampanyctus* and *Lobianchia* do the pectoral fins attain some degree of specialization.

Three characters that are shared by the larvae of many lampanyctine genera are: 1) the sequential development of three or more pairs of early-forming photophores, 2) the development of a series of melanophores at the dorsal and at the ventral margins of the body, particularly in the tail region, and 3) the development of one or more melanophores above the brain. The sequence of development of early-forming photophores is an especially useful character that may provide a key to the elucidation of phylogenetic lineages within the Lampanyctinae. Eleven of the 17 genera of Lampanyctinae develop such early-forming photophores and can be grouped as follows:

Group A—Br_2, PO_5, and Vn form in that sequence; fourth pair, either PLO or VLO, form later in larval period.
- *Scopelopsis* - VLO fourth pair to form.
- *Notoscopelus* - PLO fourth pair to form.
- *Lampichthys* - PLO fourth pair to form.

Group B—Br_2, Vn, PLO, and PO_5 form sequentially; photophores very small.
- *Ceratoscopelus* - all four pairs formed early in larval period.
- *Bolinichthys* - some species develop larval photophores, as above, and others develop only the Br_2 as larvae.
- *Lepidophanes* - Vn, PLO, and PO_5 form almost simultaneously after the Br_2; OP_1, and OP_2 form just before transformation.

Group C—Br_2, PLO, and PO_5 early-forming.
- *Lampadena* - Br_2, PLO, and PO_5 appear sequentially; later in larval period, PO_1 and Vn form sequentially.
- *Lampanyctodes* - Br_2, PLO, and PO_5 formed on 9.2-mm larva; smaller larvae and, consequently, information on sequence of appearance, not available.

Group D—Br_2, PO_5, and PO_1 early-forming.
- *Gymnoscopelus* - Br_2, PO_5, and PO_1 form sequentially, early in the larval period; much later, the VO_1 and then PO_2 appear.
- *Diaphus* - two species groups; *D. theta* and relatives form Br_2, PO_5, PO_1, VO_1, PO_2, OP_2, VO_5, PO_3, PO_4, VLO sequentially; *D. pacificus* and relatives form Br_2, PO_5, PO_1, PO_2, PVO_1, PO_3, VO_1, sequentially; photophores added gradually in *Diaphus* larvae with transformation at small size.
- *Lobianchia* - Br_2, PO_1, PO_5, PVO_1, PVO_2 form sequentially.

The above groupings suggest phylogenetic affinities which, in most cases, are supported by other characters of the larvae and adults. The sequential development of the Br_2, PO_5, and Vn photophores is unique to the genera of Group A (*Scopelopsis*, *Lampichthys*, *Notoscopelus*). The arrangement of primary photophores, so conspicuous in the transforming specimens of *Scopelopsis*, affirms the close relationship of this genus

with *Notoscopelus* and *Lampichthys*, since the three genera are the only myctophids with horizontal POL photophores on the posterior lateral surface of the body. *Scopelopsis* and *Notoscopelus* have either two or three such photophores in a horizontal line below the lateral line, while in *Lampichthys* the two horizontal photophores form a right angle with a third POL that is placed midway between the two upper POL's and the ventral series. Other characters of the larvae substantiate the close relationship of these three genera. The larvae are similar in shape of the eye, head, and body. *Scopelopsis* and *Lampichthys* have extremely similar pigment patterns and differ only in the number and size of the melanophores in each area (Figures 1-3, 5). *Notoscopelus* differs only slightly from the other two, in its lack of a melanophore in the ventral midline below the pectoral fin and in having a prominent series of melanophores along the lateral line (Figure 6).

Characters of the adults affirm the close relationship of the three genera. *Scopelopsis* and the several species of *Notoscopelus* have the highest numbers of dorsal fin rays, 21-23 and 22-27 respectively, in the family. The Dn light organ at the anterodorsal margin of the orbit is composed of two contiguous structures in *Scopelopsis* and *Notoscopelus*; it consists of a small photophore, with a margin of black pigment, dorsal to a larger opaque mass of tissue that lacks marginal pigment. In *Lampichthys* a mass of black tissue lies below the opaque luminous tissue, which extends posteriad over the entire dorsal surface of the orbit. *Scopelopsis* is covered entirely by small secondary photophores, as is the body of *Lampichthys*. Such photophores are absent from the head of *Lampichthys;* however, the four or five prominent cheek photophores of *Lampichthys* are comparable to those of *Scopelopsis*. A single opaque patch of luminous tissue lies below each pectoral fin base in *Scopelopsis*. In *Lampichthys*, a luminous patch is present in exactly the same position; however, several additional patches are present on the lateral surfaces of the body. In *Notoscopelus*, luminous patches are much more extensive, although the prominent patch below the base of each pectoral fin is present in all species of the genus.

The sequential development of the Br_2, Vn, PLO, and PO_5 is unique to the genera in group B (*Ceratoscopelus, Lepidophanes, Bolinichthys*); this, along with the small size of the photophores, and their early appearance, points to close relationship of the three genera. The larvae of some species of *Bolinichthys* are an exception, since they develop only the Br_2. Other characters of the larvae, such as a similarity in body shape and a general paucity of pigment, also suggest the close relationship of the three genera (Figures 7, 8, 9). Paxton (1972) has pointed out a number of osteological characters of the adults that link the three genera, and the similarity in the arrangement of luminous patches among species of the three genera is well established in the literature.

The larvae of *Lampadena* and *Lampanyctodes* (group C above) develop the Br_2, PLO, and PO_5. The PLO photophores become conspicuously developed on small larvae of *Lampadena* soon after the formation of the Br_2 pair; the PO_5 pair appear shortly thereafter (Figure 10). The Vn pair is later-forming and may be preceded by the PO_1 pair, or the two pairs may form simultaneously. The sequence of development of early-forming photophores on *Lampanyctodes hectoris* has not been fully established. The Br_2, PLO, and PO_5 pairs were well developed on the smallest larva (9.2 mm) available for study (Figure 11). A 14.5-mm transforming specimen of *Lampanyctodes* had 13 pairs of photophores developed, including the Vn and PO pairs. Even so, the only genera with this combination of three early-forming photophores are *Lampadena* and *Lampanyctodes*. Also, the larvae of the two genera are similar in body shape and in pigmentation.

The larvae of *Gymnoscopelus* (group D above) form the Br_2, PO_5, and PO_1 early (Figure 12). Later in the protracted larval period, the VO_1 and then PO_2 appear. In some species (e.g., *G. aphya*) the larvae reach a length of 28 mm and are the largest of all myctophid larvae. *Diaphus* and *Lobianchia* also develop the Br_2, PO_5, and PO_1 early in the larval period and are included in group D. This, however, is virtually the only larval character that the two genera share with *Gymnoscopelus*. They develop photophores grad-

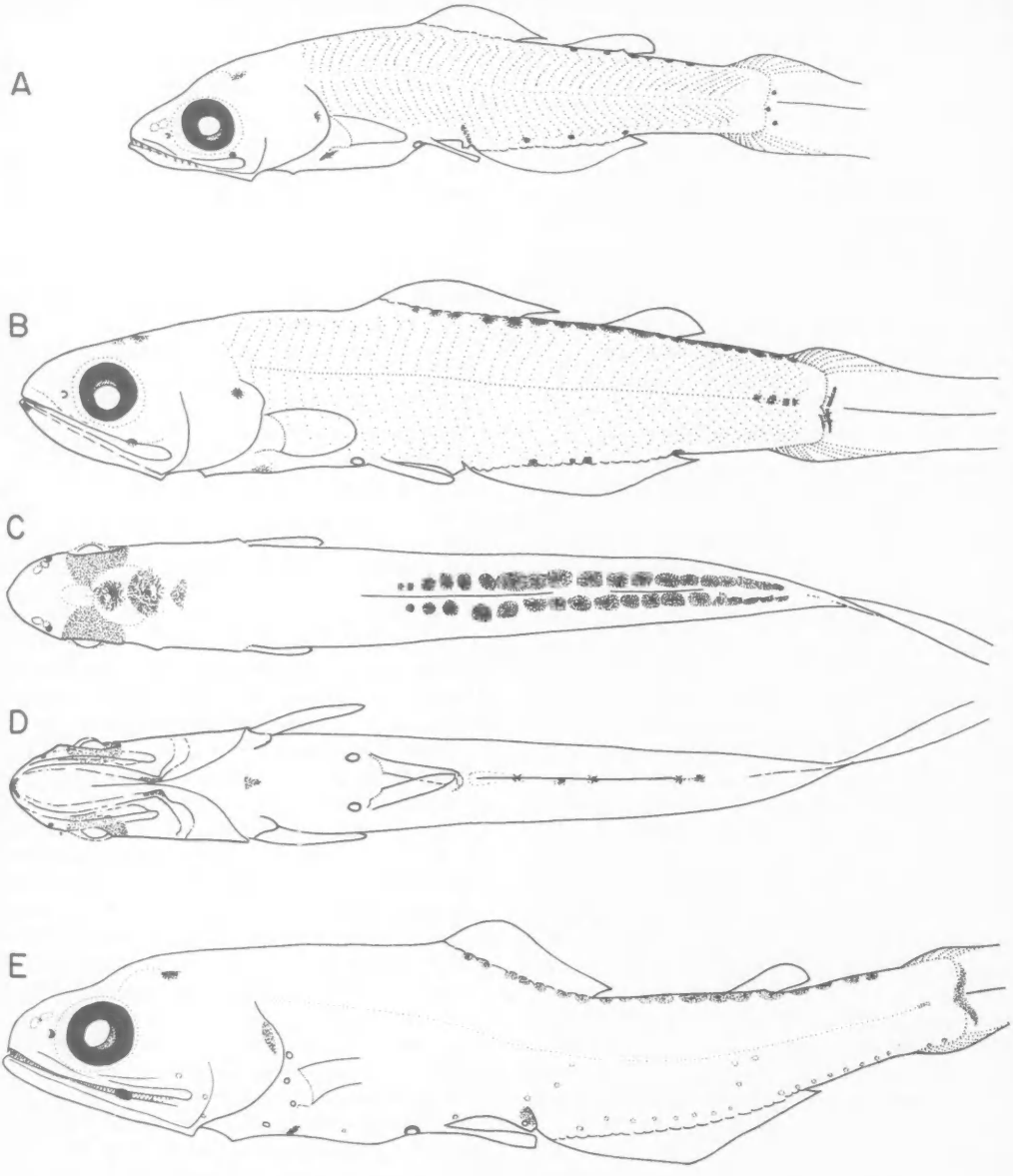

FIGURE 5.—Developmental stages of *Lampichthys procerus* (Brauer).—A, 11.4-mm larva, U.S. NS *Eltanin* Station 314; B, 14.5-mm larva, R.R.S. *Discovery* Station 100c; C, 14.5-mm larva dorsal view; D, 14.5-mm larva, ventral view; E, 20.3-mm transformation stage, U.S. NS *Eltanin* Station 306.

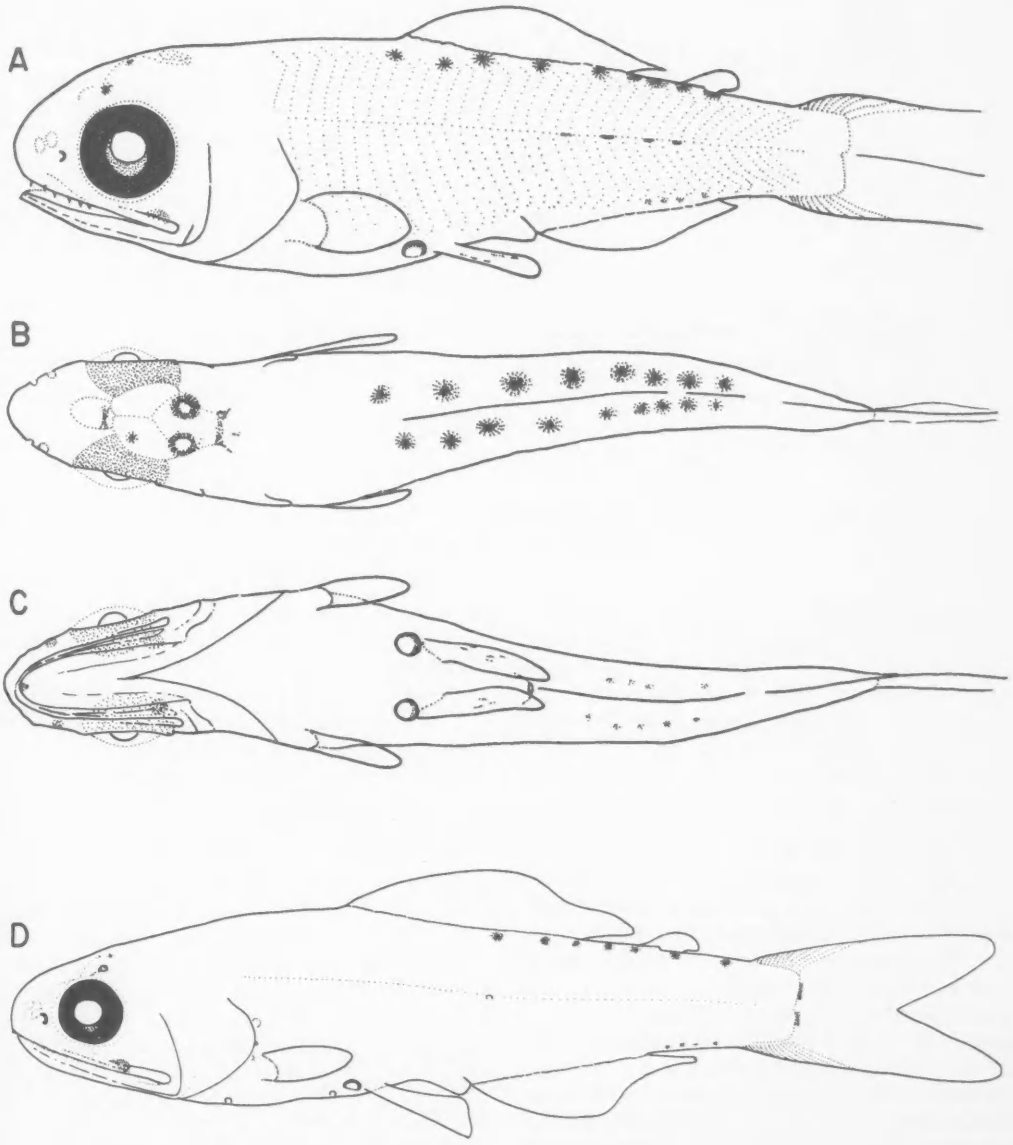

FIGURE 6.—Developmental stages of *Notoscopelus resplendens* (Richardson).—A, 11.2-mm larva, CalCOFI 6310-97.90; B, 11.2-mm larva, dorsal view; C, 11.2-mm larva, ventral view; D, 21.0-mm transformation stage, CalCOFI 6207-90.110.

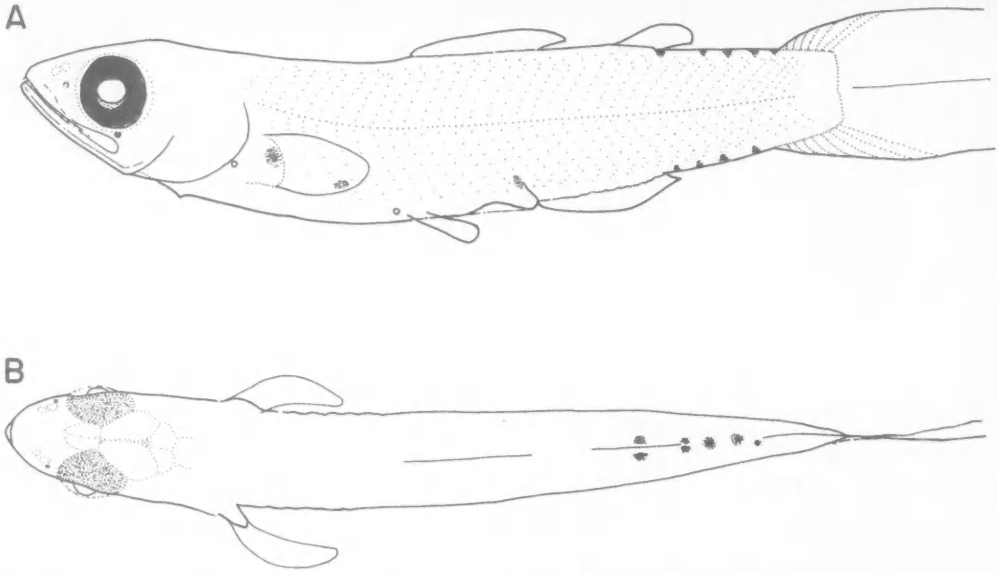

FIGURE 7.—Developmental stage of *Ceratoscopelus maderensis* (Lowe).—A, 13.4-mm larva, RV *Meteor* Station 72-39; B, 13.4-mm larva, dorsal view.

ually during the larval period, which appears to be rather short; most species transform within the size range of 10-15 mm. Also, the characteristic shape and basic pigment pattern of larval *Diaphus* and *Lobianchia* are distinctively different from those of *Gymnoscopelus*. In shape and pigmentation, the larvae of *Gymnoscopelus* resemble most closely those of group A (*Scopelopsis, Lampichthys, Notoscopelus*).

Of the remaining six genera of the subfamily Lampanyctinae, *Notolychnus* develops no photophores during the larval period, and *Lampanyctus, Triphoturus*, and *Stenobrachius* develop only the Br_2 as larvae. Our developmental series of *Taaningichthys* is incomplete; however, larvae up to 18 mm long have no photophores. In our largest larva (19.3 mm), the PO_5 are just beginning to develop. The larvae of this genus are apparently neustonic, and this may have an important influence on photophore development. They are most similar to larvae of *Lampadena* in pigment pattern but are much more slender. The small larvae of *Taaningichthys minimus* are unusual in having a conspicuous series of embedded melanophores above the vertebral column (Figure 13). The larvae of *Hintonia* are as yet unknown.

From our studies of the larvae of the subfamily Lampanyctinae, the genera *Scopelopsis, Lampichthys, Notoscopelus, Gymnoscopelus, Ceratoscopelus, Bolinichthys, Lepidophanes, Lampanyctodes, Lampadena*, and *Taaningichthys* emerge as a natural assemblage based on sequence of photophore development, morphology, and pigmentation. The grouping of these genera as a phylogenetic unit conflicts with the phylogenetic scheme proposed by Paxton (1968, 1972). His arrangement of the 17 genera of the subfamily Lampanyctinae into four tribes, based on a combination of adult osteology and photophore pattern, is shown in Figure 14. We agree that *Notolychnus valdiviae* has an ample array of unique adult and larval characters to warrant its placement in the monotypic tribe Notolychnini. Likewise we concur with the establishment of a separate tribe Diaphini for *Diaphus* and *Lobianchia*, two genera with a dis-

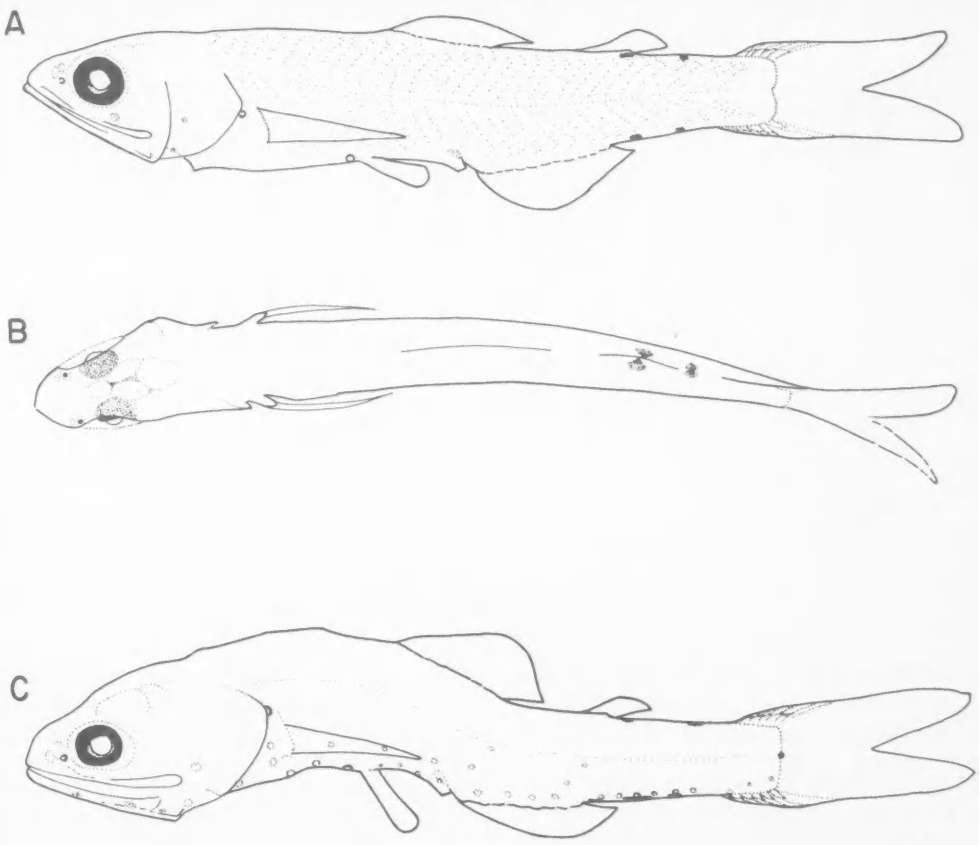

FIGURE 8.—Developmental stages of *Lepidophanes guentheri* (Goode and Bean).—A, 13.5-mm larva, R.S. *Dana* Station 3998X; B, 13.5-mm larva, dorsal view; C, 12.7-mm transformation stage, R.S. *Dana* Station 3998X.

tinct facies of adult and larval characters. Paxton placed the remaining 14 genera into two tribes, the Lampanyctini and Gymnoscopelini. On the basis of larval characters, we cannot concur with his distribution of genera among the two tribes. He included eight genera (*Lampanyctus, Stenobrachius, Triphoturus, Ceratoscopelus, Lepidophanes, Bolinichthys, Taaningichthys,* and *Lampadena*) in the tribe Lampanyctini and restricted the tribe Gymnoscopelini to six genera (*Gymnoscopelus, Lampanyctodes, Notoscopelus, Lampichthys, Scopelopsis,* and *Hintonia*). Paxton found no single character that would differentiate any of the four tribes from all others in the subfamily and relied on a combination of osteological and photophore characters to define the tribes. His most trenchant characters separating the Gymnoscopelini from the Lampanyctini were the presence of a supramaxillary bone in the Gymnoscopelini and its absence in the Lampanyctini and the presence of a Dn photophore in the former and its absence in the latter.

Our findings in the larvae suggest a different distribution of genera for the two tribes. On the basis of larval characters described earlier

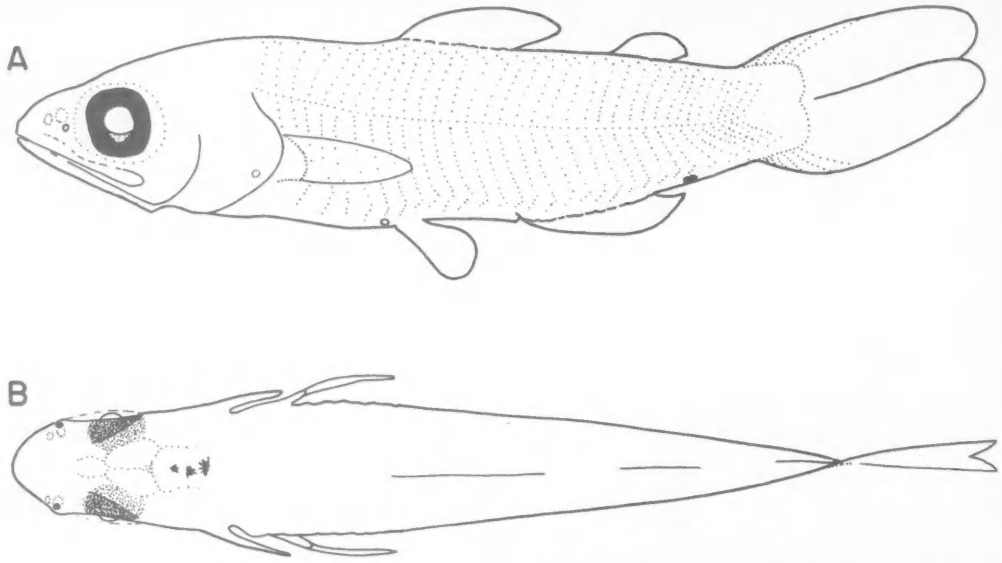

FIGURE 9.—Developmental stage of *Bolinichthys* sp.—A, 10.6-mm larva, R.R.S. *Discovery* Station 702; B, 10.6-mm larva, dorsal view.

we would enlarge the tribe Gymnoscopelini to include *Ceratoscopelus, Lepidophanes, Bolinichthys, Lampadena,* and *Taaningichthys* as well as the six genera assigned to the tribe by Paxton. We would restrict the tribe Lampanyctini to *Lampanyctus, Stenobrachius,* and *Triphoturus,* three genera with distinctive larvae that develop only the Br_2 photophores, and are characterized by an abrupt transformation from larva to juvenile. Our suggested modification of Paxton's scheme is shown in Figure 15.

Even though we propose a different distribution of genera in the tribes Gymnoscopelini and Lampanyctini, there is a striking concordance between our groupings of related genera and Paxton's, derived from quite different criteria. For example, both methods suggest a close relationship for *Scopelopsis, Lampichthys,* and *Notoscopelus* as well as for *Ceratoscopelus, Lepidophanes,* and *Bolinichthys.*

It should be noted that the heaviest development of accessory luminous tissue occurs in the genera we place in the tribe Gymnoscopelini and that such luminous tissue is best developed on *Ceratoscopelus, Bolinichthys, Lepidophanes, Lampichthys,* and *Hintonia.* On *Ceratoscopelus townsendi* and various species of *Bolinichthys,* conspicuous patches of luminous tissue form on the head between the orbits, especially in adult males. In these genera there may be a direct relation between the absence of the Dn photophores and the presence of accessory luminous tissue on the head.

A PROPOSED THEORY FOR THE EVOLUTION OF PHOTOPHORE PATTERN IN MYCTOPHIDAE

Perhaps the most intriguing result of our studies of larvae of the tribe Gymnoscopelini is a theory for the evolution of photophore pattern in lanternfishes. The only previous theory was proposed by Bolin (1939) and fully developed by Fraser-Brunner (1949). Fraser-Brunner (1949) postulated an hypothetical ancestral myctophid with a pair of continuous photophore rows on the ventral margin, beginning with the

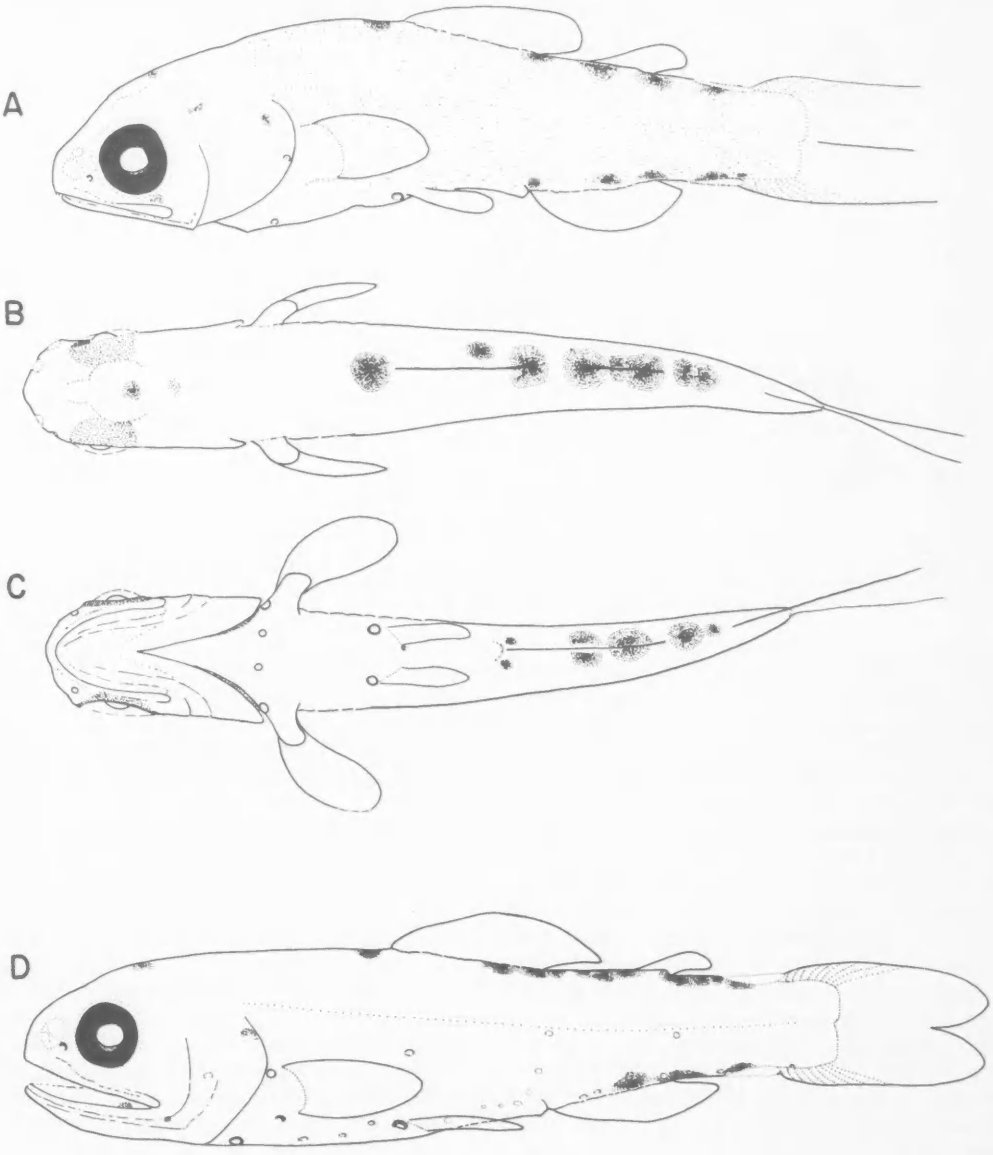

FIGURE 10.—Developmental stages of *Lampadena urophaos* Paxton.—A, 13.4-mm larva, CalCOFI 5011- S-T3; B, 13.4-mm larva, dorsal view; C, 13.4-mm larva, ventral view; D, 19.6-mm transformation stage, CalCOFI 6210-117.90.

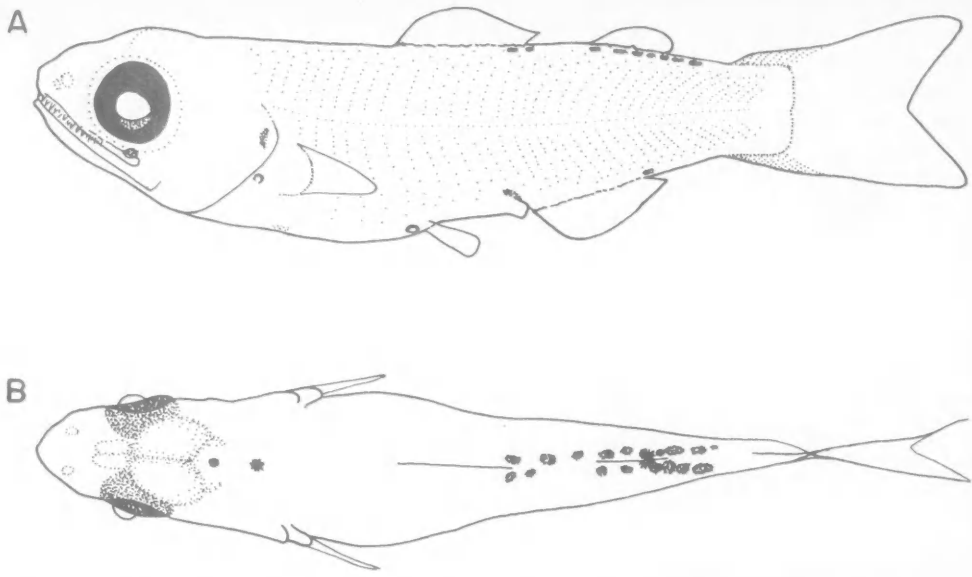

FIGURE 11.—Developmental stage of *Lampanyctodes hectoris* (Günther).—A, 9.2-mm larva, R.R.S. *Discovery* Station 1374; B, 9.2-mm larva, dorsal view.

most ventral jaw photophore (Br_3) and extending posteriad to the tail. Above these ventral rows on each side was a lateral row that extended from the middle jaw photophore (Br_2) posteriad to the anus. A third row began with the upper jaw photophore (Br_1) and ended with the upper opercular photophore. Fraser-Brunner proposed that the photophore patterns of all extant lanternfish species were derived by upward migration of certain photophores on the ventral and lateral rows of the ancestral form. His chief evidence for such upward migration was that, in present-day myctophids, certain lateral photophores, such as the posterior two SAO and the POL, lie above gaps in the ventral series. These gaps were presumably produced by the upward migration of photophores to the lateral position they now occupy. He found other indirect evidence in the presence of small modified scales which overlie certain of the lateral photophores in some species. Since these scales were out of the meristic lines of the larger scales, Fraser-Brunner concluded that they were scales that had been "taken with" the photophores during their upward migration.

Fraser-Brunner's (1949) hypothesis has remained unchallenged or at least tacitly accepted by workers up to the present; however, we believe that it contains a number of deficiencies which warrant an alternative theory for the evolution of the photophore pattern in lanternfishes. Firstly, we believe that the presence of certain lateral photophores above gaps in the ventral row is tenuous indirect evidence of migration, since there are many examples of lateral photophores lying directly above photophores in the ventral series, and there are equally numerous examples of gaps in the ventral series with no overlying photophores whatsoever. Further, we find the presence of small specialized scales over certain of the lateral photophores to be inconclusive evidence of upward migration from the ventral series, since some lateral photophores are overlain by normal-sized scales that are aligned with the other scales in their row. Also, if a photophore had carried its scale with it dur-

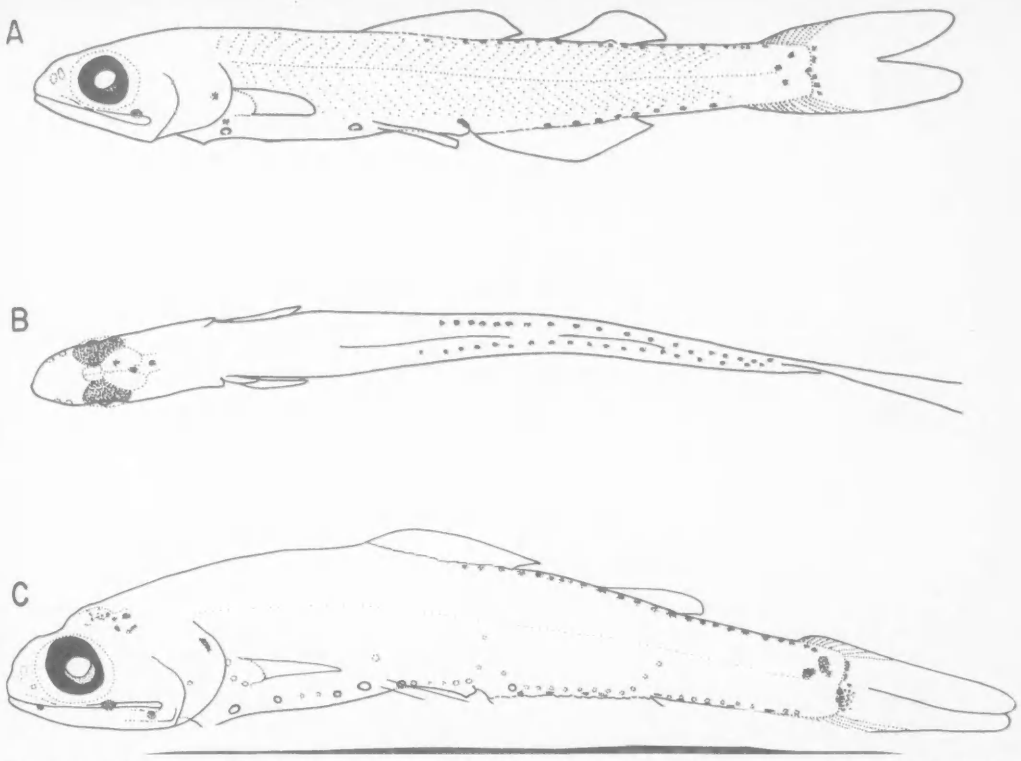

FIGURE 12.—Developmental stages of *Gymnoscopelus aphya* Günther.—A, 23.5-mm larva, U.S. NS *Eltanin* Station 319; B, 23.5-mm larva, dorsal view; C, 27.7-mm transformation stage, U.S. NS *Eltanin* Station 1341.

ing its upward migration, one might expect a comparable deletion or modification at its origin in the ventral scale row. There is none. Another major deficiency in the theory is its inability to explain the photophore pattern of a species such as *Notolychnus valdiviae* which has four pairs of photophores near the dorsal midline. If derived from the ventral series, the dorsal photophores would be supplied by peripheral nerves of the ventral or medial spinal rami that would have to extend dorsad across the horizontal septum; such an arrangement seemed so unlikely for species with photophores above the lateral line that we traced the nerve supply to such photophores in *Triphoturus mexicanus*, *Bolinichthys* sp., and *Notolychnus valdiviae*. In *T. mexicanus* the VLO, SAO_3, POL_2, and Prc_3 lie above the lateral line, and in *Bolinichthys* the latter three photophores lie above the line. These light organs are supplied by a branch of the lateral vagus nerve, the superficial lateral-line nerve. In *Notolychnus* the VLO, SAO_3, POL_2 and Prc_2 lie extremely high on the body near the dorsal midline. The VLO and SAO_3 are supplied by the dorsal ramus of the lateral vagus nerve. The nerve supply to the POL_2 was difficult to determine but appeared also to be the dorsal ramus of the lateral vagus nerve. The Prc_2 is innervated by the superficial lateral-line nerve.

Ray (1950), in her detailed study of the peripheral nervous system of *Stenobrachius leucopsarus*, showed that all body photophores, except three pairs, are supplied by ventral rami of spinal nerves. The exceptions, SAO_3, POL, and Prc_4,

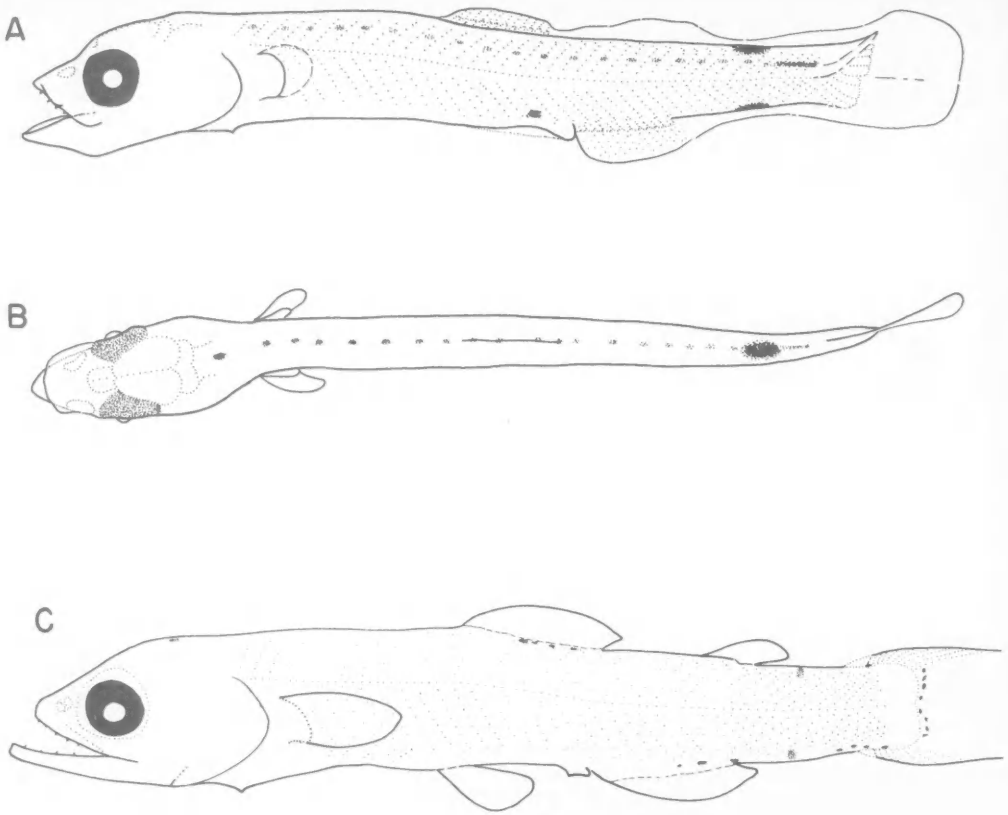

FIGURE 13.—Developmental stage of *Taaningichthys minimus* Tåning.—A, 7.3-mm larva, Hawaii Institute of Marine Biology, China Hat Series 3; B, 7.3-mm larva, dorsal view; C, 14.4-mm larva, SIO-FCRG Cruise 71-2.

are innervated by medial rami of spinal nerves; however, the first two of these each receive a small ramulus from a ventral spinal ramus. Ray believed that the innervation of lateral body photophores by ventral components of spinal nerves supported Bolin's (1939, p. 131-132) suggestion that lateral body photophores were derived by upward displacement of certain photophores from a single pair of ventral photophore rows. In lanternfish, such as *T. mexicanus*, *Bolinichthys*, and *Notolychnus*, the photophores which lie above the lateral line have always been considered homologous to their counterparts that lie below the line in other genera. Our finding of a cranial nerve supply for photophores above the lateral line in *T. mexicanus*, *Bolinichthys* sp., and *Notolychnus* casts considerable doubt on the theory that these photophores could have arisen from upward displacement, "from a primitively ventral and strictly linear series" (Bolin, 1939, p. 131-132) or even from "two ventrally located, parallel series of photophores, such as we find in *Vinciguerria*" (Bolin, 1939, p. 97).

An alternative hypothesis for the evolution of photophore patterns became apparent to us when studying the transforming stages of *Scopelopsis* (Figures 2, 3). It is obvious that in these specimens, the so-called primary photophores

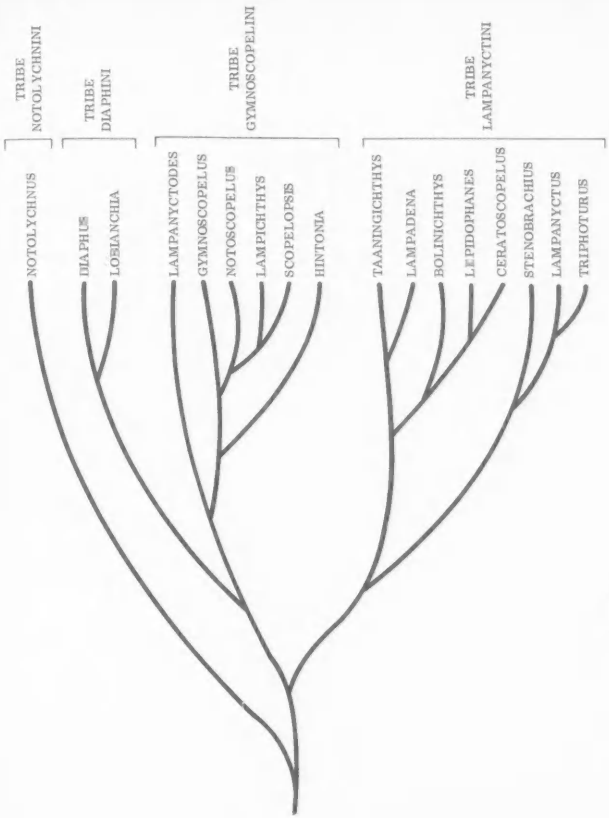

FIGURE 14.—Dendrogram of Paxton's (1968, 1972) arrangement of genera and tribes in the subfamily Lampanyctinae.

take their places very properly in the horizontal lines of smaller secondary photophores that cover the body. In these remarkable specimens, the primary photophores appear merely as enlarged members in the meristic series of light organs. Accordingly, it is tempting to speculate that this reflects a possible ancestral stage in the evolution of myctophid photophore patterns. We postulate that the archetypal pattern of light organs in lanternfishes was a generalized arrangement consisting of a single unspecialized photophore at the posterior margin of each scale pocket and a series of similar photophores distributed over the head. The progressive enlargement and specialization of certain photophores of the generalized pattern and concurrent diminution or loss of the "secondary" photophores would seem a propitious mechanism for adaptation and subsequent species diversification. The enlargement of photophores in the ventral midline to form a pair of longitudinal rows was universal in the family. Clarke (1963) suggested that these downward oriented photophores emit a continuous light of ambient wavelength which conceals the fish by breaking up its silhouette, that would otherwise be easily detected by predators hunting from below. This and other theories for the universality of the ventral photophore rows are discussed by McAllister (1967). The placement of the ventral and lateral photophores in a pattern unique to each species is an obvious mechanism for species recognition and reproductive isolation (Harvey, 1952, 1957; Marshall, 1954; Bolin, 1961).

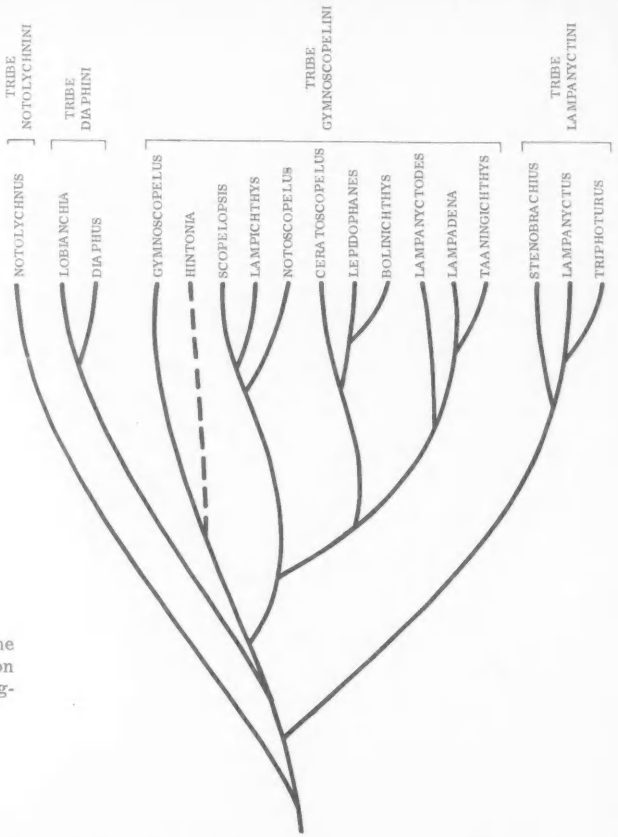

FIGURE 15.—Dendrogram showing the generic relationships and tribal division of the subfamily Lampanyctinae as suggested by larval characters.

Whatever were the adaptive forces that marshalled the light organs of myctophids into specific patterns, we believe that the ancestral myctophids had unspecialized photophores distributed over the head and body (one at the margin of each scale pocket) and that the specific patterns were derived by enhancement of some photophores and the concomitant deletion of others. Among the 28 known genera of myctophids are six (*Scopelopsis, Hintonia, Lampichthys, Bolinichthys, Lepidophanes,* and *Lampanyctus*) in which at least some species have minute photophores on the body, in addition to the typical pattern of primary photophores. The minute photophores may occur at every scale pocket (e.g., *Scopelopsis*) or may be restricted to a certain region of the body (e.g., *Hintonia*). Typically, those species with such minute photophores also have one or more head photophores that are lacking in most other myctophids. Previous workers have considered the minute photophores of these genera to be secondary structures, which have evolved after the primary organs; however, we believe that they reflect an ancestral stage in the evolution of photophore pattern. We believe that *Scopelopsis* most closely approximates the photophore pattern of ancestral myctophids since the distinction between "primary" and "secondary" organs is less apparent than in the other genera retaining secondary photophores. Moreover, every photophore position described for lanternfishes has its counterpart in *Scopelopsis*, and we find that every known myctophid photophore pattern can be generated

by enhancement of selected photophores of this species. Such a mechanism for the evolution of photophore pattern seems much less cumbersome than the theory of upward migration of photophores from the ventral series. The minor upward displacement of some ventral photophores may be a plausible explanation for the slightly arched AO and VO rows found in some myctophids but, for reasons outlined above, we find it improbable that such a mechanism could be responsible for the profoundly diverse photophore patterns of contemporary lanternfishes.

ACKNOWLEDGMENTS

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THE FISH FAMILY MORIDAE IN THE EASTERN NORTH PACIFIC WITH NOTES ON MORID OTOLITHS, CAUDAL SKELETONS, AND THE FOSSIL RECORD

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ABSTRACT

Four species of morids (*Antimora microlepis, Microlepidium verecundum, Physiculus nematopus*, and *P. rastrelliger*) are known to inhabit waters of the eastern North Pacific. These can be differentiated by numerous external and internal characters including fin-ray counts, dentition, head shape, gill-raker counts, vertebral counts, and otoliths. *Microlepidium grandiceps* and *Physiculus longipes* were found to be junior synonyms of *M. verecundum* and *P. nematopus*, respectively.

Only three characters appear to be infallible for recognizing members of family Moridae: large fontanelles in the exoccipitals through which elongate hornlike projections of the swimbladder extend and contact the auditory capsules; the otoliths; and the caudal skeleton. Otoliths and the caudal skeleton were used in evaluating the fossil record, and none of the 10 species that have been accepted as being morids, but which were known only from skeletal imprints, could be proven to be correctly identified. On the other hand, four species known only from fossil otoliths are unquestionably morids.

Morid otoliths are so distinctive and so characteristic that they appear to be reliable for distinguishing many species and most, if not all, genera. Based upon an examination of sagittal otoliths from 15 morid genera it was possible to distinguish four natural groups. These were designated the *Mora*-group containing *Mora, Halargyreus, Antimora*, and *Lepidion*; the *Physiculus*-group containing *Physiculus, Gadella, Tripterophycis, Brosmiculus, Laemonema*, and *Microlepidium*; the *Pseudophycis*-group containing *Pseudophycis, Auchenoceros, Lotella*, and *Salilota*; and the *Actuariolum*-group containing *Actuariolum*, a genus known at present from two species of extinct Miocene morids and one species living in the Antarctic.

The capture of a juvenile *Physiculus rastrelliger* off Eureka and the finding of their otoliths in a Pliocene deposit near the southern shore of Humboldt Bay aroused the curiosity of one of us (Barker) regarding the past and present distribution of this small morid. Every avenue we investigated led to frustration in the form of erroneous or unreliable information that had been perpetuated and compounded through the years. What appeared to be a 1- or 2-day project became a major undertaking just to satisfy a mild curiosity.

Unfortunately, before he was able to do much more than lay the groundwork for this study, Lloyd Barker lost his life at sea while acting as an official observer for the California Department of Fish and Game on a sea lion catching boat that sank near Santa Rosa Island. Although many of the problems were discussed prior to Lloyd Barker's death, all errors, omissions, and oversights are the sole responsibility of the senior author.

Morids generally were unrecognized and unaccepted at the family level until Svetovidov (1948) pointed out for the third time the uniqueness of the swim bladder connection with the auditory capsule, a character that was infallible for distinguishing morids from other gadoids. In a subsequent study, Svetovidov (1967) distinguished additional morid genera and further

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established the validity of the "swim bladder and fontanelle" character, while other workers publicized equally stable characters in the morid caudal complex (Rosen and Patterson, 1969) and the sagittal otoliths (Schmidt, 1968; Karrer, 1971).

In spite of such common knowledge, the validity of characters used for distinguishing genera has not been demonstrated, and any estimate of speciation would be wild at best. Perusal of available literature indicates that perhaps 20 morid genera are recognized from among the 25 or so available names. Since about half of these genera are monospecific, it seems highly probable that a critical study would result in a substantial reduction.

We limited our research to those morids inhabiting the eastern North Pacific for three reasons: (i) it is the faunal region of greatest immediate concern to West Coast fishery biologists and ichthyologists, (ii) study material was readily available, and (iii) the problems appeared to be solvable in the time we were able to budget for the study. Our work with morid otoliths and the fossil record stems from a long-seated interest in these two subjects, and knowledge of the otoliths and the caudal complex was needed in order to interpret the fossil record.

KEY TO GENERA AND SPECIES OF MORIDAE IN THE EASTERN NORTH PACIFIC

1. Snout projecting well beyond mouth as a flat, pointed rostrum; first ray of first dorsal filamentous, longer than head; 57 to 58 vertebrae; 36 to 38 caudal rays; a small oval patch of teeth on head of vomer ..... *Antimora microlepis*

   Mouth terminal, snout not flattened nor projecting; first ray of first dorsal not produced, equal to less than one-half head length; 43 or fewer vertebrae; 32 or fewer caudal rays; vomerine teeth absent or forming a single row, never in clumps or patches 2

2. Pelvic rays 2; vomerine teeth in a single row across head of vomer; 39 to 42 rays in second dorsal; 39 to 42 rays in anal; 44 to 46 vertebrae; no black fossa (luminous area) on belly between and behind pelvic fin bases ..... *Microlepidium verecundum*

   Pelvic rays 6 or 7; no teeth on vomer; 52 to 67 rays in second dorsal; 56 to 67 rays in anal; 52 to 55 vertebrae; a black fossa on midline of belly behind pelvic fin bases 3

3. Pelvic rays 6; gill rakers 16 to 19, 12 to 14 on lower limb; caudal rays 22 to 25; black fossa on belly round, width equal to length or nearly so; chin and throat densely scaled, rough to touch ..... *Physiculus nematopus*

   Pelvic rays 7; gill rakers 26 to 30, 18 to 22 on lower limb; caudal rays 27 to 32; black fossa on belly over twice as long as wide; chin and throat naked or with a few embedded scales, smooth to touch ..... *Physiculus rastrelliger*

SPECIES ACCOUNTS

Antimora microlepis Bean, 1890

D. 4(4-5),[a] 50(50-55)[a]; A. 37(39-42)[a]; C. 37; P. 20; P_2. 6(6-7)[a]; Br. 7; rakers on first gill arch 5 + 15 = 20; posterior rakers on first gill arch 3 + 12 = 15; vertebrae including hypural 24-25 + 33 = 57-58.

There is a small round patch of teeth on the head of the vomer; those in the jaws are villiform and in several rows. The broad depressed snout forms a spadelike rostrum with sharp lateral margins. The mouth is inferior. The elongate barbel at the tip of the lower jaw is conspicuous. The filamentous first ray of the first dorsal fin is more than twice as long as the next longest ray. The second dorsal and anal fins are deeply indented posteriorly and terminate adjacent to the ninth from last vertebra, including the hypural. The caudal rays com-

[a] Counts in parentheses are from Clemens and Wilby (1961).

mence adjacent to the sixth from last vertebra.

Schroeder (1940) reported that *A. viola, A. microlepis,* and *A. rhina* are synonyms of *A. rostrata* (Günther, 1878), and Clemens and Wilby (1961) and Fitch and Lavenberg (1968) followed this decision in reporting *Antimora* from the eastern North Pacific. Unfortunately, few of the characters used by Schroeder to support his action are of value for combining (or distinguishing) taxa at the species level. Type localities for *A. rostrata, A. viola, A. microlepis,* and *A. rhina* are the Indian Ocean, the western Atlantic, off Queen Charlotte Island, and off Panama, respectively. In view of the great distances separating these type localities, and until material from all four areas can be examined critically and compared in minute detail, we prefer to retain *microlepis* for the *Antimora* found in the eastern North Pacific.

A. microlepis has been reported as ranging from Central America (Fitch and Lavenberg, 1968) to Misaki, Japan (Svetovidov, 1948), but we have not seen material from south of Mazatlán, Mexico, or from west of the Bering Sea. Although we examined more than 50 individuals from the eastern North Pacific for key characters, we recorded meristic data on only one, a small specimen (LACM[4] 30400-2) trawled near San Clemente Island, Calif.

Microlepidium verecundum (Jordan and Cramer, 1897)

D. 7-9, 39-42; A. 39-42; C. 29-32; P. 19-22; P_2. 2; Br. 7; rakers on first gill-arch 5-6 + 11-13 = 17-19; posterior rakers on first gill-arch 3 + 11-12 = 14-15; vertebrae including hypural 11-12 + 33-34 = 44-46.

About seven teeth in a single row form a gently curved bow on each side of the head of the vomer. The lower jaw contains a single row of conical, sharply pointed teeth; in the upper jaw, there are two rows of teeth near the center and three irregular rows along the sides; all jaw teeth are similar in size and shape. A barbel is present at the tip of the lower jaw, but this is so tiny and inconspicuous it often can be located only with the aid of a microscope. The dorsal and anal fins terminate adjacent to the eighth from last vertebra, including the hypural; the caudal rays commence adjacent to the fifth from last vertebra.

[4] Institutions containing specimens studied are listed with standard abbreviations in Acknowledgments.

TABLE 1.—Proportional measurements for three species of morids found in the eastern north Pacific.

Measurement[1]	*Microlepidium verecundum*	*Physiculus nematopus*	*Physiculus rastrelliger*
Standard length	51-101	93-158	79-207
Total length	1105-1126	1080-1120	1079-1124
Head length	267-283	245-285	242-290
Snout length	049-058	057-073	062-076
Maxillary length	116-125	114-136	117-136
Diameter of fleshy orbit	082-093	062-079	067-081
Longest gillraker length	025-034	018-027	018-028
Snout to first dorsal fin insertion	274-300	253-288	262-298
Snout to anal fin insertion	390-426	317-351	316-359
Snout to pectoral fin insertion	268-287	249-288	253-292
Snout to pelvic fin insertion	191-247	213-246	200-255
Pectoral fin length	208-238	161-179	143-185
Pelvic fin length	244-292	272-298	122-169
Longest ray in first dorsal fin	085-108	102-123	098-127
Longest ray in second dorsal fin	094-115	092-112	078-107
Longest ray in anal fin	099-116	092-112	077-107
Caudal peduncle depth	016-019	020-025	018-022
Peduncle length (dorsal)	108-117	048-061	069-095
Peduncle length (ventral)	108-117	048-061	069-095
Number of specimens	10	10	20

[1] Standard lengths are in millimeters; all other measurements expressed as thousandths of standard length.

Morphometric data are presented in Table 1.

The unique holotype, described as *Lepidion verecundum,* was trawled at *Albatross* station 2993 (lat 18°17′15″N, long 114°44′30″W) near Clarion Island in 665 m (364 fm); it was reported as being a "young specimen, 2¼ inches long." Subsequently, Garman (1899) noted that in a specimen "only three and one-half inches in length, its ovaries are filled with eggs that appear to be about mature." We examined a female 83.5 mm SL that was running ripe in January and have seen females as small as 67 mm SL with developing eggs in their ovaries. The largest specimen we have seen was 101 mm SL (112 mm TL).

M. verecundum has been captured throughout the oceanic area from just south of Cape San Lucas, Baja California (lat 22°45′N), to about 322 km SW of Pta. San Telmo (lat 15°57′N) and offshore to Clarion Island (lat 114°44′30″W). Within this area they have been taken with midwater trawls fished well beneath the surface, and

their remains have been found in the stomachs of deep-feeding predators.

In describing *Lepidion verecundum*, Jordan and Cramer (1897) reported "dorsal VIII-40; anal 37; ventral apparently 1 (some rays broken on each side)." A radiograph of the 51-mm-SL holotype (USNM 47748) revealed that these counts should be D. 8, 39; A. 40; P_2. 2; in addition there are 19 pectoral rays, 30 caudal rays, 7 branchiostegals, and 45 vertebrae of which 12 are precaudals.

In describing the genus *Microlepidium*, Garman (1899) made several erroneous observations on the specimens he examined. He reported a "V-shaped single series of teeth on the vomer" (the single series is slightly bowed or crescent-shaped), ventral fins comprised of four rays (there are only two), and no barbel (a barbel is present, though microscopic). He noted that his *M. grandiceps* could be "distinguished from *M. verecundum* Gilb. [sic] by the larger number of rays and the shallower notch in the anal fin, the greater length of ventrals, pectorals and maxillary, and the larger number of scales in a longitudinal series." His report of "A. 4" for *M. grandiceps* is obviously a typographical error, and since the radiograph of the holotype of *Lepidion* [=*Microlepidium*] *verecundum* showed 40 anal rays, this character is negated for distinguishing the two. The other characters Garman used for separating *M. grandiceps* from *M. verecundum* are equally without basis in fact, and since we were unable to find even slight variance between the two, we relegate *M. grandiceps* to the synonymy of *M. verecundum*.

We have examined material of *M. verecundum* from the following localities, all off Mexico; lat 22°51′30″N, long 108°14′W, 12 Nov. 1967, *Velero* 11750, 1 spec.; lat 22°45.2′N, long 110°00.7′W, 16 Jan. 1969, *Alaska* 69A1-11, 2 specs.; lat 21° 13.8′N, long 107°08′W, 18 June 1952, SIO66-411, 1 spec.; lat 20°56.2′N, long 108°44′W, 16 May 1960, SIO63-979, 1 spec.; lat 20°21′N, long 106° 10′W, 19 Jan. 1970, *Velero* 13759, 3 specs.; lat 20°16′N, long 111°32.2′W, 19 Apr. 1954, SIO54-88, 7 specs.; lat 19°54.1′N, long 108°38.9′W, 18 May 1960, SIO63-981, 3 specs.; lat 19°52′N, long 113°20.5′W, 21 Apr. 1954, SIO54-92, 13 specs.; lat 18°41′N, long 111°00′W, 20-21 Apr. 1954, SIO54-91, 26 specs.; lat 18°41′N, long 110°51′W, 18 Feb. 1971, *Searcher* 57, LACM 31751-3, 1 spec.; lat 18°17′15″N, long 114°44′30″W, 6 Mar. 1889, *Albatross* 2993 (x-ray of holotype examined); lat 15°57′N, long 105°56′W, May 1968, remains of 16 fish including otoliths in stomachs of *Dosidicus gigas*.

Physiculus nematopus Gilbert, 1890

D. 9-11, 57-67; A. 62-67; C. 22-25; P. 23-25; P_2. 6; Br. 7; rakers on first gill-arch 4-6 + 12-14 = 16-19; posterior rakers on first gill-arch 3-5 + 10-13 = 14-17; vertebrae including hypural 13-14 + 38-40 = 52-53.

There are no teeth on the vomer and palatines; those in the jaws are villiform and in bands. A round block fossa, reportedly a luminous organ, lies on the midline of the belly about opposite the posteriormost base of the pelvic fins. The chin and throat region are densely scaled and rough to the touch. The dorsal and anal fins terminate adjacent to the sixth from last vertebra, including the hypural; the caudal rays commence adjacent to the fourth from last vertebra.

Morphometric data are presented in Table 1.

Jordan and Evermann (1898) designated specimens labeled USNM 46486 and 46555 as lectotypes from among the material collected in the Gulf of California by the *Albatross*. *P. nematopus* ranges from the northern Gulf of California (lat 30°26.3′N) to the Gulf of Panama (lat 07° 06′15″N) and has been captured at depths ranging from 76 to 1,271 m. Specimens from depths greater than about 366 m probably are captured well off the bottom; juveniles particularly are often taken in or near the scattering layer. The largest individual we have seen was 170 mm SL (189 mm TL).

Although *P. nematopus* was described from material dredged in the Gulf of California north of La Paz (*Albatross* stations 2997, 3011, 3015, and 3016), Goode and Bean (1895) in recording the species noted that it was found "off the southern coast of California." This erroneous statement has been perpetuated in the literature ever since (Jordan and Evermann, 1898; Jordan, Evermann, and Clark, 1930).

Garman (1899) described *P. longipes* from Panama and noted that it can be "distinguished from *Phyciculus* [*sic*] *nematopus* Gilb., by a greater number of rays in the dorsal and a smaller number in the ventrals," but the dorsal and ventral ray counts that he gave for *P. longipes* (D.10 + 55-63; V.6) are identical to counts we made on *P. nematopus*. We examined a radiograph of one of Garman's types of *P. longipes* (USNM 57876) and were unable to find any character to distinguish it from *P. nematopus*. We therefore relegate *P. longipes* into the synonymy of *P. nematopus*.

We examined material from the following localities: **Gulf of California:** 18.5 km SE of San Felipe, Feb. 1949, UCLA W49-91, 1 spec.; lat 30°26.3′N, long 114°12.1′W, 19 Jan. 1968, 76-86 m, SIO68-92, 20 specs.; lat 30°20′N, long 114°10′W, 19 Jan. 1968, 148-225 m, SIO68-93, 106 specs.; lat 29°54′N, long 113°03.2′W, 30 Mar. 1960, 110 m, SIO60-119, 6 specs.; lat 29° 19.9′N, long 113°10.4′W, 19 Jan. 1968, 265-283 m, SIO68-94, 90 specs.; lat 23°51′N, long 107°33′W, 137 m, SIO59-264, 1 spec.; lat 23° 50.5′N, long 107°18.2′W, 77-88 m, SIO59-263, 2 specs. **Costa Rica:** off Punta Quepos, Puntarenas, 16 July 1969, LACM 30721-3, 1 spec.; ±9 km off Cape Velas, 7 May 1963, UCLA W63-142, 3 specs.; near Puntarenas, UCR 490, 3 specs.; 18.5 km SW of Isla Canos, 143 m, 15 July 1969, UCR 328-6, 6 specs. **Panama:** USNM 57876, 1 spec., paratype of *P. longipes*.

Physiculus rastrelliger Gilbert, 1890

D. 8-11, 52-62; A. 56-63; C. 27-32; P. 24-28; P_2. 7; Br. 7; rakers on first gill-arch 7-9 + 18-22 = 26-30; posterior rakers on first gill-arch 4-6 + 14-20 = 18-24; vertebrae including hypural 12-14 + 40-42 = 52-55.

There are no teeth on the vomer and palatines; those in the jaws are villiform and in bands. An elongate black fossa, reportedly a luminous organ, lies on the midline of the belly about opposite the posteriormost base of the pelvic fins; it is two or three times as long as wide. The chin and throat region are naked, or at most a few scattered embedded scales are present. The dorsal and anal fins terminate adjacent to the eighth from last vertebra, including the hypural; the caudal rays commence adjacent to the fifth from last vertebra.

Morphometric data are presented in Table 1.

Jordan and Evermann (1898) designated the specimen labeled USNM 48266 as the lectotype, but did not give a locality of capture. Daniel M. Cohen (personal communication) informs us that USNM 48266 is a lot of seven specimens from *Albatross* station 3045 and that these and a single specimen (USNM 44281) from the same station are both labeled as types. *Albatross* station 3045 was at lat 26°24′N, long 113°49′W in 336.5 m (Townsend, 1901). Thus, the type locality is approximately southwest of Bahía de Ballenas, Baja California. *P. rastrelliger* ranges from 20.7 km WSW of the Mad River, Calif., (lat 40°55′N, long 124°22.5′W) to the Gulf of Panama (lat 07°12′20″N, long 80°55′W). It seldom has been captured shallower than 183 m or deeper than 366 m, but verified depths range from 128 to 523 m. The largest individual we have seen was 207 mm SL (225 mm TL).

P. rastrelliger was originally described from material dredged at *Albatross* stations 2987 and 3045, both off central Baja California. For some unknown reason, but probably an error of omission (e.g., Baja), Goode and Bean (1895), in recording this species, noted both of these stations as "off the southern coast of California." That erroneous statement very likely caused Jordan and Evermann (1898) to ascribe this species to southern California. Not until 1923 however, was *P. rastrelliger* reported from California based upon material actually taken there (Fowler, 1923). Reports subsequent to Fowler's (Ulrey, 1929; Jordan, Evermann, and Clark, 1930; Barnhart, 1936) could have been based upon any of the previous three, but probably did not involve additional Californian captures. The listing of *P. rastrelliger* by Fitch and Lavenberg (1968) was based upon numerous Californian captures of the species, not specified in detail.

We have examined material from the following localities: **California:** lat 40°55′N, long 124°22.5′W, 12 Nov. 1970, 143-146 m, *N. B. Scofield* 70S8-21, 1 spec; off Gaviota, Santa Barbara Co., 6 Aug. 1967, 263 m, SBMNH 00229, 1 spec.;

13.9 km NW of Cavern Point, Santa Cruz Isl., 23 Jan. 1961, 229 m, UCLA W61-48, 3 specs.; lat 33°58′N, long 118°43′W, 5 Aug. 1969, 320-323 m, *N. B. Scofield* 69S5-16, 2 specs.; lat 33° 57′N, long 118°39′W, 5 Aug. 1969, 283 m, *N. B. Scofield* 69S5-18, 1 spec.; lat 33°35.5′N, long 118°05.3′W, 18 Aug. 1970, 128-146 m, Oxy 70 8-18, 12 specs.; lat 33°34.2′N, long 118°04.8′W, 19 Sept. 1970, 274 m, Oxy 70 9-19, 7 specs.; lat 33°32.2′N, long 118°08′W, 27 Jan., 9 Apr., 29 Apr., and 27 Oct. 1971, 274 m, Oxy 71, 16 specs.; 6.8 km WSW of Del Mar, 12 Oct. 1950, 274 m, SIO50-249A, 6 specs.; La Jolla area, 16 and 18 Aug. 1916, Barnhart coll. D42 and D49, SIO67-138 and SIO64-287, probably the two specimens reported by Fowler (1923); 14.8 km W. of Point Loma, 21 Jan. 1965, 347.5 m, SIO65-9, 1 spec. **Baja California:** off Bahía San Quentin, 1 Apr. 1962, 183 m, SIO62-522, 3 specs.; lat 28°18.1′N, long 115°24.1′W, 247-265 m, SIO71-122; 3 specs.; lat 27°59′58″N, long 116°32′W, 20 Aug. 1967, midwater trawl, surface to 1,372 m, *Velero* 11634, LACM 30019-12, 1 spec.; lat 27°12.9′N, long 114°30.5′W, 21-22 June 1971, prawn trap 183-210 m, *Alaska* 71A5-10, 8 specs.; lat 26° 04.5′N, long 113°40′W, 2 Dec. 1960, 229-293 m, SIO60-466, 39 specs. **Gulf of California:** lat 28°19.3′N, long 112°08′W, 293-307 m, SIO68-103, 15 specs.; lat 23°07.8′N, long 109°21.3′W, 10-11 Jan. 1968, 252 m, SIO68-56, 1 spec. **Costa Rica:** vicinity of Cabo Blanco, 17-21 May 1970, 219 m, UCR 427-7, 2 specs.; off Puntarenas, UCR490, 2 specs. **Panama:** lat 07°12′20″N, long 80°55′W, 23 Feb. 1891, 333 m, *Albatross* 3355, USNM 57877, 1 spec. x-ray.

MORID OTOLITHS

Although morid otoliths were illustrated and described by Vaillant in 1888 and have been reported both in paleontological and ichthyological literature during the 20th century, Schmidt (1968) appears to have been the first to record in print their uniqueness at the family level. He illustrated sagittae from five Atlantic genera of morids and noted that "although the form of the otolith within this family is by no means uniform, it is so characteristic that one can speak of a morid type."

The characteristic which makes the morid sagitta so distinct is the deeply channeled bifurcate cauda (posterior portion of the sulcus, or groove, on the inner face of an otolith). Frost (1924) noted this character with the statement "In no other species that has passed through my hands is a double cauda to be seen," but he apparently had not seen sufficient comparative material to recognize it as being diagnostic of the family.

Karrer (1971), in an excellent treatise on morid otoliths, pointed out that the thin bladelike ridge (crista) which divides the deeply channeled cauda longitudinally is actually the posterior colliculum. She reported that the diversity of characteristics found on the morid otolith are sufficiently reliable as to permit identification of the various genera. Based upon an examination of otoliths from 13 genera (20 species), she established three natural groups of living morids: the *Mora*-group comprising *Mora, Halargyreus, Antimora,* and *Lepidion*; the *Physiculus*-group comprising *Physiculus, Gadella, Tripterophycis, Brosmiculus, Laemonema,* and *Salilota;* and the *Pseudophycis*-group comprising *Pseudophycis* and *Auchenoceros.* She hesitantly places *Lotella* with the *Physiculus*-group.

Our investigations involved otoliths from 12 genera (Figures 1 and 5), and even though we had no prior knowledge of Karrer's research, we had decided that morid otoliths fitted into the identical three groups that she described, but we added a fourth to include an Antarctic species and two New Zealand fossils. To illustrate these we had drawings prepared of *Mora pacifica, Physiculus rastrelliger,* and *Pseudophycis bachus* (Figures 2, 3, and 4), and photographed the Antarctic species and one of the fossils (Figure 5). We believe that *Lotella,* based upon the proportion of ostium length into cauda length in *L. callarias,* is more closely allied with *Pseudophycis* than with *Physiculus. Salilota* also appears to belong with the *Pseudophycis*-group.

Since morid otoliths are likely to be encountered in food habit studies, fossil deposits, and bottom sediments, and could be useful in a taxonomic revision of the family, we have construct-

ed a key for identifying to genus the sagittae we have seen. Although obviously incomplete, this key can be expanded when otolihs of the dozen or so other genera come to hand. A species-by-species discussion of these otoliths is also presented.

KEY TO OTOLITHS OF 12 MORID GENERA

1. Lower rim of cauda bowed out posteriorly creating an expanded chamber ventral to the posterior colliculum ..... (*Mora*-group) .. 2

   Lower rim of cauda straight or turned downward at tip, but never forming an expanded area posteriorly 5

2. Anterior end of sagitta greatly expanded dorsally 3

   Anterior end of sagitta not expanded dorsally; height of otolith at anterior end about the same as height at center 4

3. Ratio of otolith height into length 1:1.6 or 1:1.7 ..... *Mora*

   Ratio of otolith height into length 1:2.0 or 1:2.1 ..... *Halargyreus*

4. Ventral portion of otolith projecting beyond dorsal portion anteriorly; ventral canal of cauda only slightly expanded posteriorly ..... *Antimora*

   Dorsal portion of otolith equal in length to ventral portion anteriorly, or projecting somewhat beyond; ventral canal of cauda greatly expanded posteriorly .....*Lepidion*

5. Ostium (anterior part of sulcus) comprising approximately one-half of otolith length .... (*Pseudophycis*-group) 6

   Ostium comprising approximately one-third or less of otolith length 8

6. Anterior end of otolith greatly expanded dorsally ..... *Auchenoceros*

   Anterior end of otolith pointed 7

7. Dorsal rim of cauda longer than ventral rim; otolith knobby and greatly expanded in middle one-third ..... *Pseudophycis*

   Dorsal rim of cauda shorter than ventral rim; otolith relatively smooth middorsally, never expanded in central portion ..... *Lotella*

8. Dorsal rim of cauda about equal in length to ostium; about half as long as ventral rim .... (*Physiculus-group*) .. 9

   Dorsal rim of cauda about twice as long as ostium; more than eight-tenths as long as ventral rim ..... (*Actuariolum-group*) .. *Actuariolum*

9. Otolith with a thin shelflike blade projecting ventrally from posterior portion of inner face ..... *Microlepidium*

   No ventral projection on inner face of otolith 9

10. Otolith broadly rounded anteriorly; greatest height in anterior one-third of length *Laemonema*

    Otolith somewhat pointed anteriorly; greatest height in middle one-third ..... *Physiculus*
    Tripterophycis

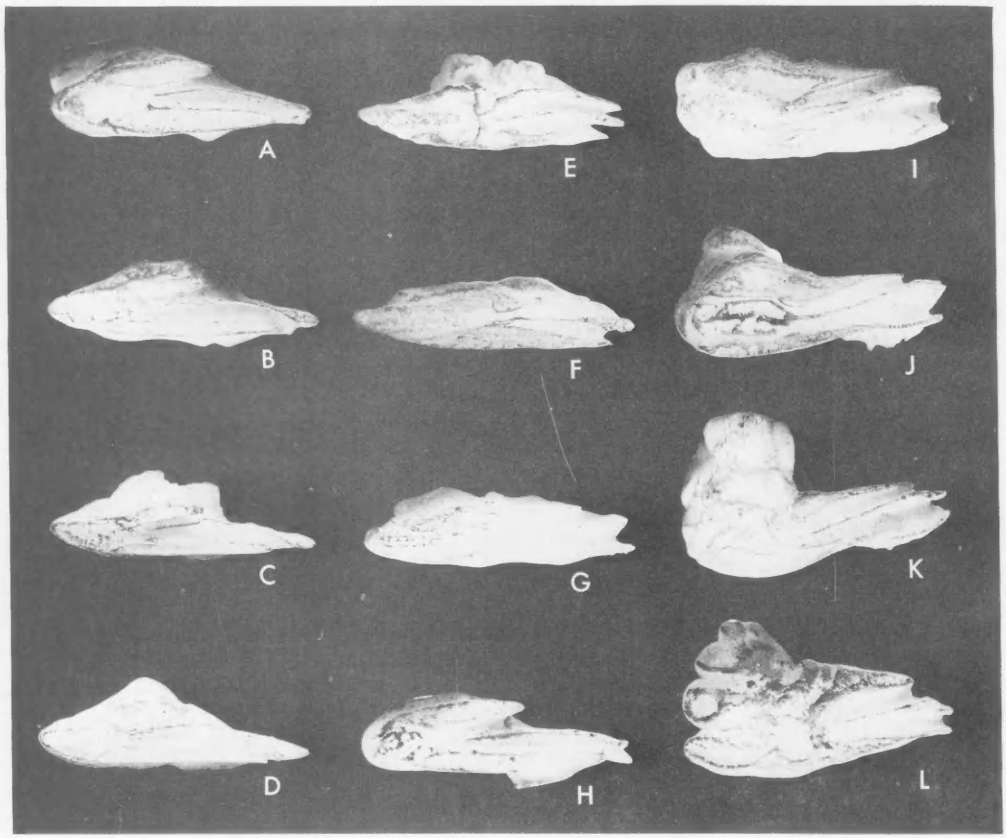

FIGURE 1.—Inner faces of right sagittae of 11 genera (12 species) of living morids: A. *Laemonema barbatulum*, B. *Tripterophycis gilchristi*, C. *Physiculus nematopus*, D. *Physiculus rastrelliger*, E. *Pseudophycis bachus*, F. *Lotella callarias*, G. *Antimora microlepis*, H. *Microlepidium verecundum*, I. *Lepidion eques*, J. *Halargyreus johnsonii*, K. *Mora pacifica*, L. *Auchenoceros punctatus*.

OTOLITH SPECIES ACCOUNTS

Mora-group (Figure 2)

Otoliths in this group are characterized by a bowing-out of the crista inferior (the ventral rim of the cauda or groove on the inner face of the sagitta), at about its midpoint, so that an expanded chamber is formed in the posterior portion of the lowermost canal. The crista superior (uppermost rim of the cauda) is more than three-fourths as long as the bladelike posterior colliculum (thin ridge which bisects the cauda horizontally). The anterior end of the sagitta may or may not be expanded dorsally. Sagittae of this group that have been illustrated are *Mora mora* (Vaillant, 1888, as *M. mediterranea;* Schmidt, 1968; Karrer, 1971); *Halargyreus johnsonii* (Fitch and Brownell, 1968, as morid #3; Schmidt, 1968, as *H. affinis;* Karrer, 1971), *Lepidion eques* (Schmidt, 1968; Karrer, 1971); and *Antimora rostrata* (Karrer, 1971).

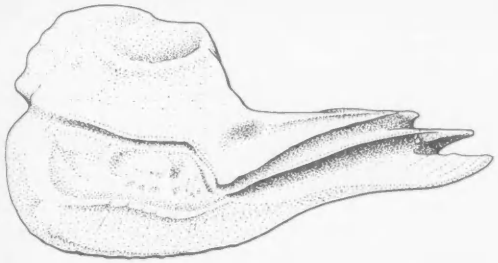

FIGURE 2.—Drawing of right sagitta from *Mora pacifica* illustrating features of *Mora*-group otoliths.

Mora pacifica *Waite, 1914* (*Figure 1K*).—In the illustrated specimen (9.5 mm long) the ostium measures 3.8 mm and the cauda, 5.7 mm. The posteriormost 3.0 mm of the ventral canal is expanded. The sagitta of *M. pacifica* (11 pairs examined) differs consistently from that of *M. mora* (5 pairs examined) in the configuration, including angles, of the expanded anterior end. In all *Mora* otoliths examined, the ratio of height into length was 1:1.6 to 1:1.7.

Halargyreus johnsonii *Günther, 1862* (*Figure 1J*).—In the illustrated specimen (11.6 mm long) the ostium measures 4.5 mm and the cauda, 6.6 mm. The posteriormost 3.2 mm of the ventral canal is expanded. In the *Halargyreus* sagittae examined (5 pairs), the ratio of height into length was 1:1.20 to 1:1.21. This ratio is sufficient to distinguish *Halargyreus* otoliths from those of *Mora*, *Antimora*, and *Lepidion*.

Antimora microlepis *Bean, 1890* (*Figure 1G*).—In the illustrated otolith (10.4 mm long) the ostium is 3.9 mm long and the cauda, 5.9 mm. The posteriormost 3.5 mm of the ventral canal is expanded. The anterior ends of *Antimora* otoliths bulge very slightly dorsally, a characteristic which was grossly exaggerated in Karrer's (1971) illustration by inadvertently rotating the otolith out of lateral alignment. *Antimora* sagittae differ from those of *Lepidion* in that the anteroventral portion is somewhat pointed and extends well beyond the anterodorsal profile. They differ from those of *Mora* and *Halargyreus* in lacking the greatly expanded anterior end. More than 30 pairs of sagittae from *A. microlepis* were examined.

Lepidion eques (*Günther, 1887*) (*Figure 11*).—In the illustrated otolith (8.0 mm long), the ostium is 3.3 mm long and the cauda, 4.2 mm. The posteriormost 2.2 mm of the ventral canal is expanded. The anterior ends of *Lepidion* sagittae (4 pairs) are somewhat squared-off dorsally and project well beyond the anteroventral angle, a characteristic which distinguishes *Lepidion* otoliths from those of *Antimora*. The generally straight dorsal profile distinguishes this otolith from those of *Mora* and *Halargyreus*.

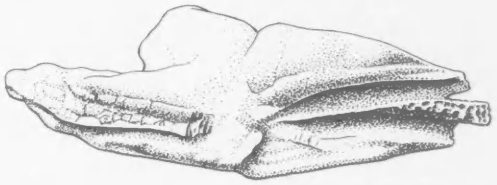

FIGURE 3.—Drawing of right sagitta from *Pseudophycis bachus* illustrating features of *Pseudophycis*-group otoliths.

Pseudophycis-group (Figure 3)

Otoliths in this group are characterized by having the ostium approximately equal in length to the cauda. The crista superior is more than three-fourths as long as the crista inferior. Greatest otolith height typically is at about mid-length, but in some (*Auchenoceros*) the anterior end is expanded (highest). Sagittae of this group that have been illustrated are *Pseudophycis bachus* (Frost, 1926, as *Physiculus bacchus;* Karrer, 1971, as *P. bacchus*), *P. barbatus* (Karrer, 1971), *P. breviusculus* (Karrer, 1971), *Lotella rhacina* (Karrer, 1971, as a member of the *Physiculus*-group), *Auchenoceros punctatus* (Karrer, 1971); and *Salilota australis* (Karrer, 1971).

Pseudophycis bachus (*Bloch and Schneider, 1801*) (*Figure 1E*).—In the illustrated otolith

(12.7 mm long), the ostium is 6.3 mm long and the cauda, 6.3 mm. In this genus, the crista superior is as long as or longer than the crista inferior, which distinguishes *Pseudophycis* sagittae from those of other genera in this group. An additional distinguishing character is the greatly expanded, knobby middorsal portion. Three pairs of *P. bachus* sagittae were available for examination.

Auchenoceros punctatus (*Hutton, 1873*) (*Figure 1L*).—In the illustrated otolith (4.7 mm long) the ostium is 2.3 mm long and the cauda, 2.4 mm. The greatly expanded anterior end easily distinguishes *Auchenoceros* sagittae from those of the other genera known to belong in this group. Two pairs of *Auchenoceros* otoliths were examined.

Lotella callarias *Günther, 1863* (*Figure 1F*).—In the illustrated otolith (11.3 mm long), the ostium is 5.7 mm long and the cauda, 5.5 mm. The combination of a pointed anterior end, a relatively smooth, unexpanded middorsal portion, and a crista superior that is shorter than the crista inferior distinguishes *Lotella* otoliths from those of other genera assigned to this group. Eight pairs of sagittae from *L. callarias* were examined.

Physiculus-group (Figure 4)

Otoliths in this group are characterized by having a relatively short ostium (comprising one-third or less of total otolith length) and a crista inferior that is almost twice as long as the crista superior. The anterior end of the sagitta usually is bluntly pointed but may be broadly rounded, it is never expanded. Sagittae of this group that have been illustrated are *Physiculus dalwigki* (Vaillant, 1888), *Physiculus peregrinus* (Kotthaus, 1970), *Physiculus capensis* (Karrer, 1971), *Physiculus* spp.? (Hatai, 1965, as *Odontobutis*; Fitch and Brownell, 1968, as morid #1 and morid #2), *Gadella maraldi* (Schmidt, 1968, as *Uraleptus maraldi*; Karrer, 1971), *Laemonema robustum* (Vaillant, 1888), *L. laureysi* (Schmidt, 1968; Karrer, 1971), *L. barbatulum* (Karrer, 1971), *Tripterophycis gilchristi* (Karrer, 1971), and *Brosmiculus imberbis* (Karrer, 1971).

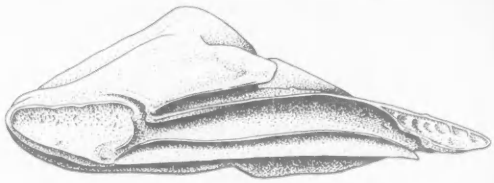

FIGURE 4.—Drawing of right sagitta from *Physiculus rastrelliger* illustrating features of *Physiculus*-group otoliths.

Microlepidium verecundum (*Jordan and Cramer, 1897*) (*Figure 1H*).—In the illustrated otolith (3.5 mm long), the ostium is 0.8 mm long and the cauda, 2.7 mm. The crista superior (1.2 mm) comprises 33% of total otolith length and is slightly less than one-half the length of the crista inferior (2.3 mm). This otolith is characterized by having a thin ventrally directed "blade" projecting from the posteriormost 40% of the inner face. Ten pairs of sagittae from *M. verecundum* were examined.

Laemonema barbatulum *Goode and Bean, 1895* (*Figure 1A*).—In the illustrated otolith (7.3 mm long), the ostium is 2.4 mm long and the cauda, 4.6 mm. The crista superior (2.1 mm long) is slightly less than one-third the total otolith length, but more than one-half as long as the crista inferior (3.5 mm). Sagittae of *Laemonema* are broadly rounded anteriorly, and by this character can be distinguished from otoliths from other genera placed in the *Physiculus*-group. Eleven pairs of sagittae from *L. barbatulum* were examined.

Physiculus rastrelliger *Gilbert, 1890* (*Figure 1D*).—In the illustrated otolith (9.6 mm long), the ostium is 2.7 mm long and the cauda, 6.7 mm. The crista superior (2.7 mm long) comprises about 28% of total length and is slightly more than half as long as the crista inferior (4.8 mm). The otolith of *P. rastrelliger* can be distinguished from that of *P. nematopus* by the width of the

flattened area immediately above the crista superior. At any given otolith length, this area is only about half as wide on *P. nematopus* sagittae as on those of *P. rastrelliger*. We were unable to find any reliable character or set of characters for distinguishing *Tripterophycis* sagittae from those of *Physiculus*, but for any given species a careful comparison on a size-for-size basis appears to have merit. More than 30 pairs of sagittae from *P. rastrelliger* were examined.

Physiculus nematopus *Gilbert, 1890* (*Figure 1C*).—In the illustrated otolith (7.5 mm long), the ostium is 2.2 mm long and the cauda, 5.3 mm. The crista superior (2.2 mm long) comprises approximately 29% of total otolith length and is slightly more than half as long as the crista inferior. As in other species of *Physiculus*, the anterior end is almost conical in lateral outline. The lumpiness of the outer face is highly variable and is of no value for distinguishing species. Such lumps are always more pronounced on otoliths of juveniles than adults. Ten pairs of sagittae from *P. nematopus* were examined.

Tripterophycis gilchristi *Boulenger, 1902* (*Figure 1B*).—In the illustrated otolith (8.0 mm long), the ostium is 2.4 mm long and the cauda, 5.5 mm. The crista superior (2.2 mm long) comprises about 28% of total otolith length and very slightly exceeds half the length of the crista inferior (4.3 mm). Sagittae of *Tripterophycis* are very difficult to distinguish from those of other genera placed in the *Physiculus*-group that have conical anterior ends. Fifteen pairs of sagittae from *T. gilchristi* were examined.

Actuariolum-group (Figure 5)

Otoliths in this group are characterized by having a relatively short ostium (comprising one-third or less of total otolith length), a crista superior that is about three-fourths as long as the crista inferior, and an expanded anterior end. Sagittae which have been illustrated from this group are *A. bicaudatum* (Frost, 1924, as *Physiculus bicaudatus;* Karrer, 1971) and *A. terakohensis* (Frost, 1933, as *Physiculus terakohensis*; Karrer, 1971). Both of these species are extinct Miocene fossils from New Zealand.

Actuariolum *sp.* (*Figures 5A and 5B*).—Karrer (1971) errected the genus *Actuariolum* (type species *A. bicaudatum*) for Frost's (1924, 1933) two fossils, and in corresponding with one of us (Fitch) she thought that "one day a recent species will be found which will belong to this genus or show a very close relationship." Subsequently, in examining a number of unidentified morid otoliths from cruises of the *Eltanin*, we turned

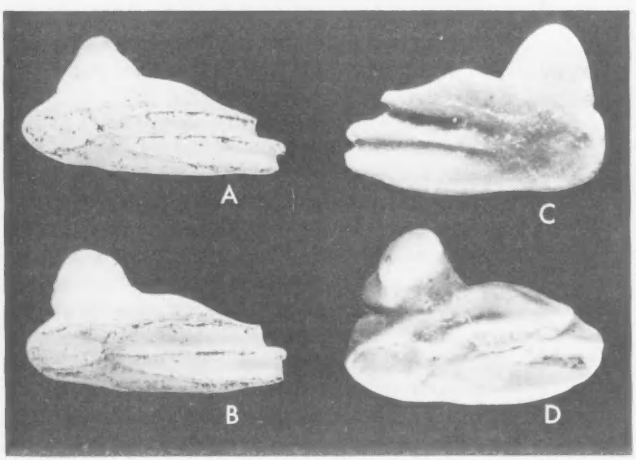

FIGURE 5.—Otoliths from *Actuariolum*: A and B, right sagittae, 5.2 and 4.2 mm long, respectively from an undescribed species collected at *Eltanin* station 1851, lat 49°40′S, long 178°53′E, 476-540 m, 3 Jan. 1967); C. and D., left and right sagittae from *A. terakohensis* collected in Lower Miocene deposits (Paratoetoe Fm.), Parengarenga Harbor, North Island, New Zealand, 2.9 and 3.0 mm long, respectively.

up several sagittae which match all salient characters of the fossil *Actuariolum*. In the illustrated specimens (from *Eltanin* station 1851, lat 49°40′S, long 178°53′E, 476-540 m) which are 5.2 and 4.2 mm long (Figures 5A and 5B) the ostium measures 1.7 and 1.2 mm; the crista superior, 2.9 and 2.6 mm; and the crista inferior, 3.3 and 2.9 mm, respectively.

For comparison, measurements of the illustrated fossil sagittae (*A. terakohensis* from the Paratoetoe Formation, Lower Miocene, Parengarenga Harbour, Figures 5C and 5D) are: total length, 2.9 and 3.0 mm; ostium, 0.9 and 1.0 mm; crista superior, 1.4 and 1.6 mm; and crista inferior, 1.9 and 1.9 mm, respectively.

Additional specimens of the undescribed species were trawled at *Eltanin* station 1411 at lat 51°00′S, long 162°01′E in 333 to 371 m. All morids from these two stations are in the U.S. National Museum fish collections (Hugh H. DeWitt, personal communication); those from station 1851 appear to represent an undescribed species.

THE MORID CAUDAL SKELETON

The morid caudal skeleton (Figure 6) not only is unique among gadoids, it is unique among teleosts. The two lowermost hypurals (1 and 2 of Rosen and Patterson, 1969) are fused at their base, which lies adjacent to the penultimate ural vertebra, but are otherwise autogenous. Above these, hypurals 3, 4, and 5 diverge posteriorly as separate entities from the ultimate ural vertebra. Among other gadoids, hypurals 1 and 2 are fused into a single plate, as are hypurals 3, 4, and 5.

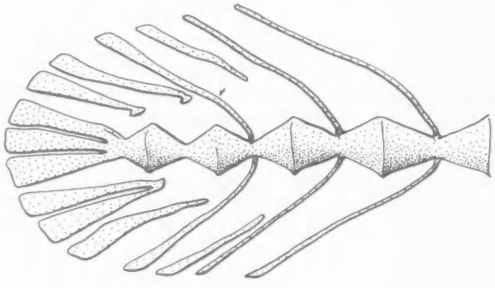

FIGURE 6.—Caudal skeleton of *Antimora microlepis*.

The remaining caudal skeleton, although typical for all morids examined, is not unique to family Moridae. Anterior to the dorsalmost hypural, there are successively: two autogenous epurals with bases adjacent to the penultimate ural vertebra, a neural spine arising from the first preural centrum, a free-floating splinter bone (dorsal accessory bone of Rosen and Patterson, 1969), and then neural spines on successive centra. Preceding the lowermost (first) hypural is an autogenous parhypural with its base adjacent to the penultimate ural centrum, a haemal spine affixed to the first preural vertebra, a free-floating ventral accessory bone, and then haemal spines on successive centra. The two epurals and the parhypural are present in most other gadoids, but the autogenous splinter bones (dorsal and ventral accessory bones) may or may not be present depending upon which gadoid genus is being examined.

Thus in any fossil skeletal imprint, if one could locate either the autogenous lowermost hypurals (1 and 2) with their fused base, or the diverging uppermost hypurals (3, 4, and 5) which project posteriorly from the ultimate ural centrum, the imprint unquestionably would be that of a morid.

FOSSIL MORIDS

The fossil record for family Moridae is based upon an abundance of skeletal imprints and otoliths, primarily from the Northern Hemisphere. Most of these were described prior to 1940, and most were placed in family Gadidae, which at that time included the morids. Danil'chenko (1953) was the first to assign fossil gadoids to family Moridae, but included *Melanonus* which Marshall (1965) subsequently removed to its its own family. In 1960, Danil'chenko suggested that *Eclipes* from the Californian Miocene was a morid, and at the same time he removed to family Brotulidae one of the species he considered a morid in 1953.

In our search for diagnostic characters which we could use to evaluate the fossil record, we found that only three features were infallible for distinguishing members of family Moridae:

the otoliths (Karrer, 1971), the caudal complex (Rosen and Patterson, 1969), and the large fontanelles in the exoccipitals through which elongate hornlike projections of the swim bladder extend and contact the auditory capsules (Svetovidov, 1948, 1967). Unfortunately, the diagnostic fontanelles cannot be distinguished in two-dimensional fossil imprints because of crushing, and three-dimensional skeletal remains are extremely rare, so one must rely upon either otoliths or the caudal complex to distinguish fossil morids.

Otoliths are abundant in most shelly marine deposits, but seldom are accompanied by other skeletal remains. On the other hand, in deposits where skeletal imprints abound, aragonitic substances, including otoliths, seldom remain. We know of only one deposit where otoliths have been found in situ in morid skeletal imprints. This is a Miocene diatomite deposit east of Los Angeles, Calif., and the morid is an undescribed species. Apparently several species examined by Danil'chenko (1960) from the Maikop deposits also have retained their otoliths, but he did not mention finding them in morids.

The tiny diagnostic hypurals of a morid caudal complex are difficult to observe unless the fossilized skeleton is preserved in lateral aspect, and such perfectly preserved specimens are extremely rare. In many of the gadoid skeletal imprints that we have seen, the caudal is either missing or so badly fragmented as to be virtually useless for determining relationships.

In commenting on the material reported upon by Danil'chenko (1953, 1960) we have relied heavily upon information obtained from Daniel M. Cohen, who examined much of it. During a trip to New Zealand, one of us (Fitch) examined fossil otoliths in the University of Auckland collections and noted sagittae from four species of Miocene morids, including both species reported upon by Frost (1924, 1933). In addition to two unreported species in the New Zealand Miocene, we have seen morid otoliths in the Miocene of California (two species), Jamaica (one species), and Poland (one species) which have not been reported in the literature. One of the two species from California probably represents an extinct genus, but additional comparative material will need to be examined before this can be determined for certain.

STRINSIA ALATA STEINDACHNER, 1859

Danil'chenko (1953) placed this species from the Upper Miocene of Europe in family Moridae, based upon its presumed resemblance to the recent *Strinsia tinca* Rafinesque, 1810, and to one of his fossils, *Strinsia sobievi*. Subsequently, he decided that his *Strinsia sobievi* was a brotulid (Danil'chenko, 1960), and Cohen and Torchio (1964) showed that Rafinesque's *Strinsia tinca* (the type species) was a macrourid. A search for Steindachner's *S. alata* in Vienna during April 1971 was unsuccessful (Daniel M. Cohen, personal communication). On the basis of published information it is not possible to associate *S. alata*, described from a poorly preserved partial skeletal imprint, with family Moridae.

ONOBROSMIUS ELONGATUS (KRAMBERGER, 1883)

Onobrosmius (type species *Brosmius elongatus* Kramberger, from the Upper Miocene of Croatia) was proposed by Bogachev (1938) for fossil cods with a single dorsal fin, which is separated from the caudal fin by a small interval. The absence of teeth on the vomer and palatines was weighted heavily by Danil'chenko (1960) in assigning *Onobrosmius* to family Moridae, but none of the characters he reported for this fossil genus or any of the species assigned to it is diagnostic for the family. It very likely is a gadoid, but its acceptance as a morid must await examination of material on which any of several diagnostic characters are clearly evident.

PHYSICULUS RASTRELLIGER GILBERT, 1890

Fitch (1969) reported finding otoliths from *P. rastrelliger* in Pliocene deposits at Los Angeles, San Pedro, and Newport Beach, Calif. In two of the three deposits that yielded *Physiculus* sagittae, they were the most abundant otoliths

present, representing 27 and 10% of the total otolith yield. Subsequently, Zinsmeister (1971) reported otoliths of *P. rastrelliger* from one of these same two deposits (LACM Invert. Paleo. Loc. 471) but did not give data on numerical abundance. One of us (Fitch) has found otoliths of *P. rastrelliger* in other southern Californian Pliocene and Pleistocene deposits at San Diego (LACM Invert. Paleo. Loc. 305), Newport Beach (Jamboree Blvd.), and near Rincon Point, Santa Barbara County (Bates Road), and a Centerville Beach locality (south Humboldt Bay) investigated by Barker also has yielded fair numbers. The Centerville Beach deposit appears to be of Pliocene age and represents the farthest north the species has been found.

ECLIPES VETERNUS JORDAN AND GILBERT, 1919

The type specimen of *E. veternus*, now in the California Academy of Sciences collection, is an incomplete (tail missing), poorly preserved skeletal imprint with the head rotated into a different alignment than the body. Jordan and Gilbert (1919) placed this small fish in family Apogonidae, but did not feel strongly regarding this assignment. Subsequently, Jordan (1921) moved it into family Gadidae, where it was retained by David (1943). Danil'chenko (1960), although he did not examine the type, felt that the genus *Eclipes* was much more closely related to family Moridae than Gadidae. However, the characters he used to support this opinion are not unique to the morids, either by themselves or in combination.

A careful examination of the type specimen revealed that not only is the type description wholly unreliable, there is no character or combination of characters that will permit assigning this small fish to any gadoid family. Only because of its small size, flattened anterior neural spines, and the shape, placement, and extent of its dorsal and anal fins can it be associated with other fossil gadoids in the Miocene diatomites and shales of California. Since *E. veternus* is the type species of *Eclipes*, but is not a morid, the name *Eclipes* is not available for use in family Moridae.

MERRIAMINA ECTENES JORDAN AND GILBERT, 1919

The identity of this little fish presents an enigma. In describing *M. ectenes*, Jordan and Gilbert (1919) placed it in family Brotulidae and designated specimen number XIII as the type. Their caption for Figure 1, Plate XXVII (Jordan and Gilbert, 1919) reads "*Merriamina ectenes* Jordan & Gilbert; type XIII (El Modena)," but the illustrated slab (Figure 1) clearly is labeled "XII."

In checking Jordan's fossils in the California Academy of Sciences collection we found their specimen XIV (Figure 3, Plate XXVII), which now bears in Lore David's handwriting the inscription "*Merriamina ectenis* [*sic*] type El Modena = *Eclipes veternus*," but we were unable to locate the type (XIII), the illustrated "type" (XII), or specimen CVII from which Jordan and Gilbert obtained their vertebral count. In the text (p. 56-57), they mentioned examining seven different specimens of *M. ectenes* and gave numbers for each of these, but "XII," the specimen illustrated as the type, is not listed, which leads us to believe that the use of "XIII" in the text and figure caption might have been a typographical error. In any event, the photograph of specimen XII (Figure 1, Plate XXVII) shows a poorly preserved gadoid-like fish with what is obviously a regenerated caudal fin. Thus, if specimen XII is in fact the type, *Merriamina ectenes* cannot be assigned to a family with any certainty, even though Jordan (1921) subsequently declared *M. ectenes* a synonym of *Eclipes veternus* and placed it in family Gadidae.

Jordan and Gilbert's other illustrated specimen (XIV), part of the type series, has hypural elements 3, 4, and 5 fused into a single plate, so it cannot be a morid (E. H. Ahlstrom, personal communication).

ECLIPES MANNI JORDAN, 1921

An examination of the caudal complex on Jordan's type specimen (No. 543), now in the California Academy of Sciences collection, revealed that hypurals 3, 4, and 5 are fused into

a single plate. For this reason, *E. manni* can not be assigned to family Moridae.

Although Jordan (1921) reported that the beautifully preserved type is "17½ inches long," and David (1943) lists it as being "355 + 35 = 390 mm [15½ inches] in length," we found that it measures only 339 mm SL (13⅜ inches), or 378 mm TL (14⅞ inches). David's measurement can be duplicated by including the lower jaw and by failing to note where the caudal rays actually terminate. Unfortunately, the lower jaw became disarticulated and moved forward during fossilization, so it cannot be used as a point of reference in measuring total length. On the other hand, the caudal appears to terminate 31 mm behind the hypural, but upon careful scrutiny it can be seen that one or more of the uppermost rays extend for 38 mm behind the hypural.

David's (1943) description of *E. manni* was based on a composite of several specimens representing at least two species and should be regarded as generally unreliable for characterizing the species.

ECLIPES EXTENSUS JORDAN, 1921

The type specimen of *E. extensus* (Jordan's No. 716) is the "tail only of a long and slender fish." The hypural elements are in such a poor state of preservation that we were unable to determine what direction was dorsal, an opinion shared by E. H. Ahlstrom (personal communication). It appears to be a gadoid, but there are no characters which will permit assignment to a particular gadoid family. The long slender vertebrae and strong neural and haemal spines differ strikingly from those found in the other three species ascribed to genus *Eclipes*.

ACTUARIOLUM BICAUDATUM (FROST, 1924)

In describing this otolith from New Zealand, Frost (1924) noted that it "resembles in a remarkable way the otolith of the living New Zealand species *Physiculus* [= *Pseudophycis*] *bacchus* [*sic*]." The broadly triangular, flared anterior end of this fossil resembles superficially the configuration of *Auchenoceros* sagittae, but the very short ostium precludes its being congeneric. Karrer (1971) proposed the name *Actuariolum* for this fossil and placed it in her *Pseudophycis*-group, but we believe the very short ostium of the fossil sagitta negates affiliation with *Pseudophycis*. In fact *A. bicaudatum* has sufficient anomalous characters to warrant establishing a separate group for it and *A. terakohensis* (Frost, 1933). The type series (three otoliths) is from a Pukeuri road cut, north Otago, in the Rifle Butts Formation, Awamoan Stage, Pareora Series and is Lower Miocene in age (J. A. Grant-Mackie, personal communication).

ACTUARIOLUM TERAKOHENSIS (FROST, 1933)

This otolith described (as *Physiculus terakohensis*) from "the unique holotype" is the basis for dating family Moridae from the Oligocene (Berg, 1940). Karrer (1971) recognized its erroneous placement with *Physiculus* and assigned it to her new genus *Actuariolum*. The holotype is from the Golden Bay Cement Company's marl pit at Tarakohe, Nelson, in the Tarakohe Mudstone, Altonian Stage, Southland Series which is Lower Miocene in age, not Upper Oligocene as originally reported by Frost (J. A. Grant-Mackie, personal communication).

While in New Zealand, one of us (Fitch) examined more than a dozen otoliths of *A. terakohensis* in the University of Auckland collections. All of these were from the Paratoetoe Formation (Lower Miocene) at Parengarenga Harbor on the North Island; otoliths associated with them included myctophids, berycids, bregmacerotids, macrourids, gonostomatids, congrids, and other deepwater forms as well as a few shallow-water species.

LOTELLA ANDRUSSOVI (BOGACHEV, 1933)

This species was assigned to genus *Brosmius* by Bogachev (1933) on the assumption that it had but a single, elongate undifferentiated dorsal fin. Danil'chenko (1953) determined that it did in fact have two dorsal fins, and because of the

two dorsal fins, a lack of teeth on the vomer and palatine bones, and other similarities with his fossil *L. smirnovi*, he placed it in genus *Lotella*. The type specimen (from middle Miocene) is in the form of a well-preserved double impression about 90 mm long, but lacking the anterior part of the head (Danil'chenko, 1960). Two other specimens, from the Tarkhan Beds of the Kerch Peninsula, were available to Danil'chenko (1960), but his description fails to mention the dentition. Positive assignment to family Moridae will necessitate finding a skeletal imprint with otoliths in situ or with a discernible morid caudal complex. Even then it cannot be assigned to *Lotella* unless the dentition that is characteristic of this genus can be observed.

ECLIPES SANTAMONICAE DAVID, 1943

The type specimen of *E. santamonicae* (David's No. 10223), now in the collection of the Natural History Museum of Los Angeles County, is a badly fragmented, poorly preserved gadoid, on which indelible brown ink has been used to draw in missing parts and to highlight others. Not only has the type slab been retouched, the photograph of the altered type (Figure 4, Plate 5: David, 1943) has been further retouched.

A careful comparison of the types of *E. santamonicae* and *E. manni* leads us to believe that they are conspecific; thus, *E. santamonicae* is relegated to the synonymy of *E. manni*. It is not a morid.

ONOBROSMIUS OLIGOCAENICUS BOGACHEV, 1938

Danil'chenko (1960) noted a marked similarity between some species of *Onobrosmius* and the fossil species referred to *Lotella*, and reported that among the few but conspicuous differences between *Onobrosmius* and *Lotella* are a slightly bipartite dorsal fin, wider pectorals, and particularly a greater number of pelvic fin rays in *Lotella*. Interestingly, he ascribed eight pelvic fin rays for both *L. smirnovi* and *L. andrussovi*, whereas he noted "V 7-8" for *Onobrosmius oligocaenicus*.

As with the description of *O. elongatus*, no character reported for *O. oligocaenicus* is diagnostic for family Moridae. *O. oligocaenicus* occurs in the Zuramakent Horizon, Upper Maikop, and according to Danil'chenko (1960) the fauna of this horizon cannot be compared with the fossil fauna of any other region, so the problem of its absolute geologic age remains obscure. Although the Zuramakent Horizon has been variously placed in Lower Miocene and Upper Oligocene, we believe from available evidence that it could be no older than Lower Miocene at most.

LOTELLA SMIRNOVI DANIL'CHENKO, 1953

In assigning this species to *Lotella*, Danil'chenko overlooked the very characteristic dentition of the genus: an outer row of widely spaced large teeth and an inner band of small teeth. According to Daniel M. Cohen (personal communication) the dentition of *L. smirnovi* is readily visible and is not as described above. Although there is nothing in the type description that would rule out assigning *L. smirnovi* to family Moridae, Daniel M. Cohen (personal communication) said that "the tail appears to have been regenerated, so I cannot be absolutely certain that it is a gadoid." In light of these anomalies it will be necessary to reevaluate *L. smirnovi* using irrefutable familial and generic characters, if such can be found on the available imprints.

L. smirnovi occurs in the same horizon as *Onobrosmius oligocaenicus*, and, as noted above, there is no substantial evidence that this horizon is older than Lower Miocene.

STRINSIA SOBIEVI DANIL'CHENKO, 1953

In his original description, Danil'chenko placed this fossil in family Moridae and stated that the holotype, a double impression 40 mm long, is similar to the Upper Miocene *S. alata* Steindachner which is known only from fragments of the head and forward part of the body. Subsequently, with additional material at hand, he designated *S. sobievi* as the type species for a new genus, *Protobrotula*, and moved it into family Brotulidae (Danil'chenko, 1960). Daniel M. Cohen examined Danil'chenko's material of this species and informed one of us (Fitch) that

"*Strinsia sobeivi* is based on very faint impressions [and]. . . I cannot say what it is." In view of the fact that the type of the genus *Strinsia* is a macrourid, that Steindachner's *S. alata* cannot be located, that Danil'chenko has moved his *S. sobievi* from family Moridae into family Brotulidae, and that diagnostic features cannot be found on the available material representing this species, it seems unlikely that this fish is a morid.

LEPIDION MIOCENICA SATO, 1962

Although this Miocene fossil from Japan probably is a gadoid and may be a morid, characters which could validate its assignment to family Moridae are either lacking or cannot be seen in the unique holotype. The vertebrae behind the second dorsal fin base are missing, otoliths are not mentioned and apparently were dissolved during fossilization, and if fontanelles ever were present in the exoccipitals they were rendered unrecognizable when this fish was crushed into a two-dimensional imprint.

In making his generic assignment, Sato (1962) states that "the present species is apparently referable to the genus *Lepidion* . . . in having [the] following important features: tail elongate and tapering posteriorly; two dorsals well developed together with the anal, and they are all composed of soft rays; anal fin is inserted far behind a perpendicular through origin of second dorsal fin base; snout is short and rather bluntly pointed in lateral view." Unfortunately, none of these characters is diagnostic of *Lepidion*, either by itself or in combination with the others. It would have been helpful to know if there were teeth on the vomer and the length of the anterior ray of the first dorsal fin (Norman, 1957).[5] Although Sato (1962) reported that the vomer was present, he failed to indicate whether it was toothed or naked. The anterior ray of the first dorsal fin is neither prolonged nor filamentous in the photograph of the type, but in his reconstruction Sato has made it filamentous.

[5] Norman, J. R. 1957. A draft synopsis of the orders, families and genera of recent fishes and fish-like vertebrates. British Museum (Natural History), London, 649 p. (Unpubl. manuscr.)

ODONTOBUTIS CF. *OBSCURA* HATAI, 1965

Apparently because of incorrectly identified comparative material Hatai (1965) assigned a "worn [morid] otolith measuring about 5 mm in length" from the Pliocene of Japan (Hamada sea cliff, Tanabu-machi, Shimo-Kita-gun, Aomori Prefecture) to family Eleotridae under the name *Odontobutis* cf. *obscura*. We do not know what species of morid he had for comparison [listed as *Odontobutis obscura obscura* (Temminck and Schlegel), and *O. o. yuriagensis* new subspecies], but the otoliths he illustrates appear to be identical to one reported by Fitch and Brownell (1968) from the stomach of a pygmy sperm whale harpooned off Japan. His fossil otolith has a bluntly rounded anterior end and differs in other features from those he affiliated it with, so it could not be identical. Based upon morid sagittae we have seen, Hatai's fossil otolith is most closely related to *Physiculus*, but correct generic placement must necessarily await comparison with morid species inhabiting the waters of Japan today. Karrer (1971) assigns this fossil to genus *Physiculus* (i.e., "ohne Zweifel der Gattung *Physiculus* angehören").

DISCUSSION

Based upon skeletal imprints, 12 fossil species have been assigned to family Moridae at various times in the past. Subsequently, one of these (*Merriamina ectenes*) was deemed conspecific with another (*Eclipes veternus*), and a second (*Strinsia sobievi*) was made the type of a new genus and moved into family Brotulidae. Our studies revealed that of the ten remaining species, one (*Eclipes santamonicae*) is conspecific with *E. manni* and three others (*E. veternus, E. manni*, and *E. extensus*) definitely are not morids. In addition we were informed that the type and only known specimen of *Strinsia alata* cannot be found, but since the tail portion of this imprint was never present and the remaining skeletal parts are not diagnostic, it could not be assigned to family Moridae even if the type were located. For the same reason (missing caudal complex), neither *Lotella smirnovi* nor *Lepidion*

miocenica can be retained in family Moridae with any certainty. Finally, the descriptions of the remaining three (*Onobrosmius elongatus*, *Lotella andrussovi*, and *Onobrosmius elongatus*) are all lacking in characteristics which are diagnostic of any gadoid family, and until or unless such features can be observed on the type specimens, the only reason for retaining them in family Moridae would be mere intuition.

Morids have also been reported in the fossil record from otoliths found in New Zealand, California, and Japan. One of these, reported as *Odontobutis* cf. *obscura* (an eleotrid) from the Pliocene of Japan, appears to represent an extant species of *Physiculus*, but no specific assignment can be made until comparative material from Japanese waters has been examined. All of the species known from otoliths are unquestionably morids.

On paleontological evidence, Danil'chenko (1960) reported that the Moridae constitute probably the oldest family of the order Gadiformes. He based this opinion on the belief that *Melanonus*, abundant in Oligocene rocks, was a morid, but Marshall (1965) removed *Melanonus* to its own family, and our investigations have revealed that none of the fossil morids, or presumed morids, is more ancient than Lower Miocene. Rosen and Patterson (1969) pointed out additional reasons for questioning morid antiquity and the logic of relating their ancestry to other gadoids.

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MARINE FISHERIES OF NEW YORK STATE[1]

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ABSTRACT

Review of the history of landings of fish and shellfish in the State of New York shows that the record since 1880 can be divided into three periods. The first was a period of development of coastal fisheries in shallow waters, which ended about 1930. The second, which lasted until the early 1950s, was a period of extension to fishing grounds farther offshore, the era of the trawl fisheries. The third was a period of steady decline in landings, still under way, characterized by a return to inshore resources.

The 90-year record has seen the rise and virtual collapse of the industrial fisheries of the State, steady decline of the oyster industry to a relatively minor status, and growth and decline of many other once-important fisheries. The variable level of total annual landings has been maintained by constant shifting from one resource to another as the stocks of each have declined in turn. This is a classic example of the evolution of a coastal fishery under a regime which offers no effective management.

Popular opinion is almost unanimous in blaming foreign fishing for the ills of the domestic fisheries. It is believed that unilateral extension of national jurisdiction would remedy the situation. In reality, although foreign fishing is not without effect, it impinges on relatively few of the coastal fishery resources of New York State. The major problems are domestic, and they will be most difficult to solve.

It seems particularly appropriate, in a volume which honors Dr. O. E. Sette, to discuss the marine fisheries of one of the northeastern States. It was in this general area that he did some of his earliest and best known scientific work, on *Scomber scombrus*, the Atlantic mackerel (Sette, 1930a, 1930b, 1931, 1932, 1933a, 1933b, 1934, 1938, 1943, 1950). It also is appropriate to use as basic data for this paper the published historical statistics on commercial fish catches, because for about 6 years Dr. Sette was Assistant in Charge of the Division of Fishery Industries in the United States Commission of Fisheries. In this capacity he was author of the annual reports of the Federal Government on commercial fishery landings (Sette, 1925, 1926a, 1926b, 1928; Sette and Fiedler, 1929).

When Dr. Sette first became responsible for gathering and publishing statistics on the commercial fisheries of the United States, only a few surveys of landings had been made and published. These began with data for 1880 and represented a few, usually widely scattered, years. The precision and completeness of these early records is questionable; but, when Dr. Sette began to gather the data for 1923, his well-known concern for accuracy and thoroughness began to be felt and his tenure in the 1920s marked the beginning of an almost unbroken series of annual reports on many aspects of the commercial fisheries of the United States, including landings by weight and value for each of the States.

Gathered, as they must be, by various indirect methods and by a relatively small force of field agents, these data cannot be completely accurate. It is obvious also that total landings are not very good indices of abundance of a species, for abundance can vary from many causes, such as changes in demand, or fishing effort, competition from other fisheries, and other economic forces. Yet no one would challenge seriously the value of these data as general indicators of trends in the fisheries and even as gross indicators of changing abundance. It is surprising that

[1] Parts of the analysis on which this paper is based were made under support of a fellowship with the Woodrow Wilson International Center for Scholars, Washington, D.C., July and August 1971.

[2] Marine Sciences Research Center, State University of New York, Stony Brook, NY 11790.

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commercial landings have not been used more frequently to describe the condition of the fisheries of an area, for, used with caution and with an understanding of their limitations, these statistics can be most revealing (McHugh and Bailey, 1957). Considered in conjunction with existing knowledge of the biology and life histories of the stocks of fish and shellfish, they also can be valuable background materials for planning research, development, and management of the fisheries and the resources upon which they depend.

For these reasons, on beginning to examine the fisheries of a region it is useful to turn to the published record. It is not enough to consider total landings. The history of each fishery must be examined, for the species composition of the catch may be very different at different points on the time scale. For example, in the State of New York, as in many States, the ranking of species in landed weight in 1880 was greatly different than in 1970. American oyster (*Crassostrea virginica*), the dominant food species in 1880, was a very minor component of the catch in the 1960s. Surf clam (*Spisula solidissima*), not recorded in the catch until about 1900 and a minor resource until about 1950, now dominates.

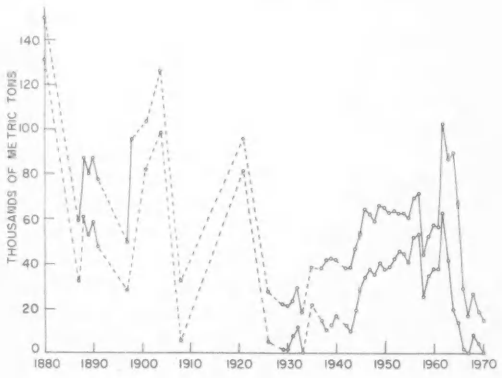

FIGURE 1.—Total annual commercial landings of fish and shellfish in the State of New York, 1880-1970. The lower line is the menhaden catch. In this, as in the other figures, broken lines have been used to join points between which one or more years' data are missing.

Examination of catches of a few years, selected at more or less regular intervals over the 90-year period, is not adequate to tell the whole story. Inevitably, some species, which were important for a while and then declined in their contribution to the total catch, will be missed. It is necessary to study the catch by species or by stock of fish for all years in which data are available. The work of Dr. Sette and his colleagues about 35 years ago, in improving the basis for collection of commercial catch statistics, has made this possible. The story that these records tell is most revealing in the light of present problems of the coastal fisheries and the steps that have been proposed to solve them.

I am indebted to Miss Karen Henrickson for her careful preparation of the illustrations.

HISTORY OF TOTAL LANDINGS IN NEW YORK

To analyze total landings intelligently the data must be separated into at least two subsets. In many coastal States, especially along the Atlantic and Gulf of Mexico coasts of the United States, industrial fishery resources dominate the marine commercial fish catch, and the history of total landings is largely a history of the industrial fisheries, primarily Atlantic menhaden, *Brevoortia tyrannus* (Figure 1). Total landings of food fish and shellfish have had a different history, which for New York apparently can be separated into three phases (Figure 2).

The first such phase, covering 1880 to 1926, was characterized by wide fluctuations in food fish landings in the State. Data are available for only nine scattered years, and their accuracy is not known, especially for the early years. The peak year in this period was 1908, with a reported food fish catch of about 54 million pounds (24,500 metric tons). More than 88% of this catch consisted of 13 genera: American oyster, weakfish (*Cynoscion regalis*), sea mussels (*Mytilus* and *Volsella* spp.), flounders (probably mostly summer flounder, *Paralichthys dentatus;* winter flounder, *Pseudopleuronectes americanus*; and yellowtail flounder, *Limanda ferruginea*), bluefish (*Pomatomus saltatrix*), Atlantic

FIGURE 2.—Annual commercial landings of food fish and shellfish in the State of New York, 1880-1970.

cod (*Gadus morhua*), hard clam or quahog (*Mercenaria mercenaria*), scup (*Stenotomus chrysops*), butterfish (*Peprilus triacanthus*), and black sea bass (*Centropristis striata*). The low year, except for 1880, was 1921, with a reported catch of about 31 million pounds (14,000 metric tons) of food fish and shellfish. About 73% of these landings consisted of oyster, flounders, weakfish, scup, bay scallop (*Aequipecten irradians*), bluefish, northern lobster (*Homarus americanus*), hard clam, cod, and butterfish. The decrease was caused largely by sharp drops in landings of weakfish and mussels, and substantial drops in oyster, cod, and bluefish landings. By 1926 food fish landings had increased again to about 49 million pounds. The increase was mostly haddock (*Melanogrammus aeglefinus*), but landings of flounders and cod increased also. These increases were partially offset by a substantial drop in oyster production, but landings of weakfish, bluefish, and lobster dropped too.

The second phase was from 1929 to 1951. Landings were reported for almost every year of this period, which was marked by a sharp increase in food fish landings from 1935 to 1938, a 15-year period in which average annual food fish landings were about 58.4 million pounds (26,500 metric tons), and an equally sharp decline from 1950 to 1953. Most of the increase from 1935 to 1938 was caused by an increase in landings of haddock, cod, flounders, silver hake (*Merluccius bilinearis*), and butterfish, species caught primarily in trawls. Production of oyster meats also increased by nearly 4.5 million pounds (2,000 metric tons) from 1935 to 1938, as the highly mechanized oyster planting industry reached its full development. This almost doubled oyster production in the State and introduced a period of prosperity in the local oystering industry which lasted for more than 15 years.

The years of highest landings of food fishes in New York State, 1938 to 1946 inclusive, were unusual years for the fishing industry everywhere. Toward the end of this period, especially, demand for fish was high because meat rationing was in effect in the later years of the war. No price controls or rationing were imposed on fishery products. Thus, fish prices were high, and the incentive to go fishing was great. For 11 of the 13 years between 1938 and 1950 inclusive New York landings of food fish and shellfish were greater than ever before or since in recorded history, and it is probable that this could be said of 1941 also, a year in which no record of landings was made. The abrupt drop in landings which began after 1946 probably was stimulated by three factors, declining prices of fish as meat became more available after the war, increasing costs, and declining abundance of some of the major species.

Declining abundance of some species was becoming evident during the war. Although demand for fish was high, and prices good, the species composition of the catch was changing during this period of maximum landings and increased fishing effort. Catches of cod, flounders, haddock, butterfish, and sea scallop dropped substantially, and oyster production was down considerably also. The high levels of catch were maintained by increases in landings of hard clam and surf clam, northern puffer or swellfish (*Sphoeroides maculatus*), weakfish, and scup. Thus, the fisheries of the State were shifting from resources taken mainly on the high seas to species of the coastal zone.

The third phase, from 1952 to 1970, was a period of gradually declining landings. In the

first 10 years of this period the average annual landings of food fish and shellfish were about 40.4 million pounds (18,300 metric tons), and in the last 9 years about 35.7 million pounds (16,200 metric tons). Species which during the war began to contribute less to the catch continued in general to decline in importance; but the most spectacular declines were the virtual collapse of the two most important fisheries of the State, the oyster and menhaden industries.

INDUSTRIAL FISHERIES

Industrial fisheries have been relatively important along the northeastern Atlantic coast of the United States for a long time, although the peak of landings was not reached until about 1955. The principal species, and for most of the period of record the only industrial fishery resource of importance, has been the Atlantic menhaden. The period of greatest development of the Atlantic coast menhaden fishery came with the decline of the Pacific sardine (*Sardinops sagax*) fishery on the Pacific coast. Indeed, the recent history of menhaden landings shows a remarkable parallel to the rise and fall of the Pacific sardine fishery, with a time lag of about 20 years (McHugh, 1969b). There is no reasonable room for doubt that the principal cause of the decline in the Atlantic menhaden fishery was overfishing, as has been established for the Pacific sardine fishery (Murphy, 1966). It would have been prudent, for want of better information, to manage the menhaden fishery in the light of the extensive historical and scientific knowledge of the sardine resource, but for various reasons this was not done. The work of Dr. Sette and his associates on the sardine resource and its fishery (see, for example, Sette, 1969) could have provided valuable guidance for research and management of menhaden fishing if it had been heeded on the Atlantic coast. The Federal Government program on the Pacific sardine was started by Dr. Sette in 1948, and the results of this work, coupled with extensive studies begun much earlier by the State of California, have provided detailed documentation of the effect of fishing on the sardine resource. Although

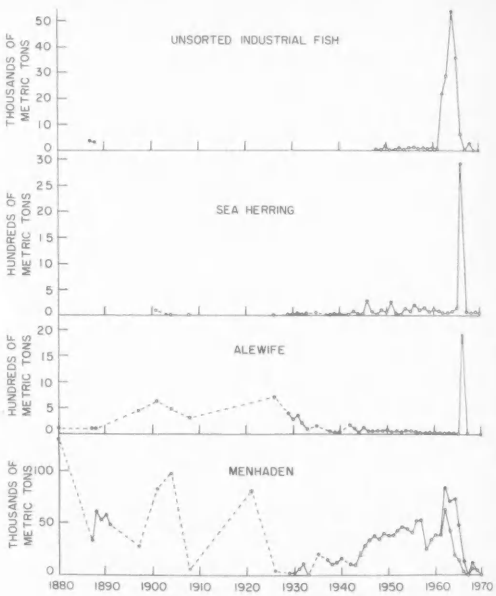

FIGURE 3.—Annual landings of industrial fishes in the State of New York, 1880-1970. The lines joining the black circles at the right of the menhaden graph represent total landings of all industrial species.

it is virtually certain that overfishing was the primary cause of the decline of both fisheries, the tendency of both resources to fluctuate widely in abundance from natural causes was an important contributing factor, which made overfishing inevitable.

The decline of the menhaden fishery north of Chesapeake Bay has been much sharper than to the southward. In New York the fishery is almost defunct (Figure 3). This decline could have been predicted with some assurance from the similarity of life histories of Atlantic menhaden and Pacific sardine and from the similar early collapse of the Pacific sardine fisheries in the north.

To state the background briefly, although both species spawn sometimes in waters near the northern parts of their ranges, the principal spawning areas are to the south, off southern California and Baja California, and to the south of Chesapeake Bay. Each year the fish make a

northward migration in spring and return in fall, and as they grow older they move farther north. Menhaden caught north of Chesapeake Bay usually are large, mature fish, most of which have had an opportunity to spawn at least once. It is probable that if menhaden fisheries had not developed south of Delaware Bay, the northern fisheries could have continued forever. It is certain that the abrupt decline in New York waters would have been slowed, if not prevented altogether. The resource would, of course, continue to fluctuate widely in abundance from natural causes, but the danger of overfishing probably would have been much less. The intense menhaden fishery in Chesapeake Bay, which now takes almost exclusively immature fish in their first and second years of life, reduces the life expectancy so greatly that few fish live long enough to migrate farther north. Thus, the collapse of the menhaden fishery in New York waters, like the early collapse of the sardine fishery in northern California and higher latitudes, was caused not so much by local overfishing, but by overfishing by other fleets in the waters of other States to the southward.

Menhaden landings in New York first began to decline in 1958. In 1959 a sharp increase in catches of menhaden in local pound nets heralded a brief increase in abundance, caused by unusually successful spawnings to the south. By 1962 menhaden landings in the State had risen to the highest level in recorded history since 1921. But the drop in 1958 had stimulated development of a new industrial fishery on mixed fish caught in otter trawls (Figure 3). This fishery for a while maintained the supply of industrial fish despite the rapid decline in menhaden landings after 1962, but the last year of substantial trawl catches of industrial fish was 1965. The decline of this trawl fishery had two principal causes, reduced abundance of fish on the grounds frequented by the fleet which was landing its catch in New York and return of most of the vessels to their home base in Rhode Island when the reduction plant at Point Judith opened (Smith, 1967).

In 1966, in a last desperate attempt to find alternate resources, the purse seine fleet made substantial catches of alewives (*Alosa pseudoharengus*) and Atlantic herring (*Clupea harengus*). The total catch of these two species (Figure 3) rose to more than 10 million pounds (4,600 metric tons), several times greater than any other year in recorded history. But this was a relatively small supply of fish for the menhaden plants, and the fishery lasted for only 1 year. The industrial fishing and processing industry of New York State has been virtually non-existent since 1966. The remaining plant on Long Island has closed, and the relatively few menhaden now caught in New York waters are taken to New Jersey for processing.

FOOD FISHERIES

As already mentioned, the history of the food fish and shellfish industry of New York State can be divided into three periods. Table 1 shows the relative and the absolute importance of the major species in four periods. It is clear even from this condensed summary that the species composition of the catch and the relative importance of many of the species have changed in complicated ways. It requires detailed consideration of each of the important species to understand how complex these changes have been and what implications are contained in this history.

Four sets of statistics were used in compiling these summaries. The illustrations are based on the Statistical Digests published annually by the Federal Government. The latest available, when background material for this paper was gathered, was Lyles (1969), which contained data for 1967. Since the 1950's the State of New York and the Federal Government have jointly published New York landings. The latest available was Smith (1971), containing data for 1970. Data on total commercial catches in the general area, including foreign catches, were taken from annual statistical bulletins compiled by the International Commission for the Northwest Atlantic Fisheries (ICNAF). The latest available was for 1968 (International Commission for the Northwest Atlantic Fisheries, 1970). The latest compilation of marine sport fish catches available was for 1965 (Deuel and Clark, 1968). Some data now are available on the 1970 marine sport fishing survey, but these could not be obtained in time for inclusion here.

TABLE 1.—Average annual landings in metric tons of major species of fish and shellfish in the State of New York for four major periods in the history of the commercial fishery of the State. Ranks by weight in parentheses.

Species	1887-1926	1929-1935	1938-1951	1952-1970
Oyster	6,085(1)	3,180(1)	3,270(2)	500(8)
Bluefish	2,360(2)	410(11)	* (25)	270(13)
Weakfish	1,315(3)	454(10)	590(13)	* (26)
Flounders	1,180(4)	2,950(2)	4,405(1)	2,860(2)
Cod	1,090(5)	1,180(4)	1,405(6)	454(9)
Shad	865(6)	135(21)	680(12)	180(17)
Hard clam	770(7)	545(9)	2,495(4)	2,250(3)
Alewife	410(8)	225(15)	* (30)	135(19)
Butterfish	365(9)	680(7)	1,225(7)	770(7)
American eel	365(10)	180(18)	90(24)	90(21)
Haddock		2,045(3)	2,770(3)	* (27)
Sea scallop		910(5)	1,045(10)	1,045(5)
Tilefish		865(6)	180(18)	* (24)
Scup		590(8)	2,360(5)	4,040(1)
Squid		365(12)	365(16)	410(10)
Atlantic mackerel		270(13)	680(11)	90(20)
Silver hake		270(14)	1,180(8)	1,135(4)
Soft clam		225(16)	135(22)	* (22)
Northern lobster		225(17)	90(23)	270(12)
Sea bass		180(19)	450(14)	270(14)
Surf clam		135(20)	1,135(9)	910(6)
Pollock		135(22)	* (28)	* (32)
Blue crab		90(23)	* (34)	* (30)
Atlantic bonito		90(24)	* (29)	* (29)
Sea mussels		* (28)	180(20)	* (25)
Red hake		* (29)	180(17)	180(16)
Striped bass		* (33)	180(19)	365(11)
Atlantic herring		* (37)	90(24)	225(15)
Northern puffer		* (58)	410(15)	180(18)
Flounders:				
Yellowtail			1,890	1,090
Winter			1,315	725
Summer			1,180	1,090

* Denotes average annual landings of less than 50 metric tons.

Domestic commercial fishery statistics are listed by States, but those of ICNAF and recreational fisheries are not. ICNAF added a new statistical area in 1966, which includes approximately the coastal and continental shelf waters from Rhode Island to Cape Hatteras, commonly referred to as the Middle Atlantic Bight. Prior to that time ICNAF statistics included only catches from Georges Bank north. Deuel and Clark (1968) reported sport fish landings by broad areas of coastal waters. Sport catches from waters off New York were included in the New England region.

For these reasons it was not possible to make direct comparisons of domestic commercial, foreign, and recreational catches for any single year. This is why the text follows the rather artificial device of comparing domestic commercial catches for 1970 with foreign catches for 1968 and recreational catches for 1965. This also is why, in comparing commercial and recreational landings, it was necessary to use the catch for the entire Atlantic coast north of Cape Hatteras.

OYSTER

Infrequent records of oyster production prior to 1929 show that landings probably were at a maximum in New York late in the 19th century and in the first decade of the 20th (Figure 4). Annual landings from 1887 to 1908 inclusive ranged from about 13 to 20 million pounds of meats (6,000 to 9,000 metric tons) and averaged over 15 million (7,000 metric tons). Thereafter, oyster production declined rather steadily

FIGURE 4.—Annual landings of oyster in the State of New York, 1880-1970.

except between 1926 and 1952 inclusive, when the trend was not obvious. Annual production in this period fluctuated between about 5 and 10 million pounds of meats (2,300 and 4,500 metric tons), and the average was somewhat more than 7 million pounds (3,200 metric tons). Although average landings in this intermediate period were only about half those reported at the turn of the century, this was in many ways the heyday of oystering in New York, despite closing of some once important grounds by pollution. Especially in Long Island Sound, this was the most highly mechanized and advanced form of oyster farming on the Atlantic and Gulf of Mexico coasts. After 1952 oyster landings in New York dropped sharply, and since 1959 annual production has been less than a million pounds of meats (less

than 450 metric tons). The low point was reached in 1967 with total production of only about 100,000 pounds of meats (45 metric tons).

The principal cause of the collapse of the New York oyster industry was a massive invasion of sea star (*Asterias forbesi*) in the 1950s. Favorable environmental conditions for this predator led to an extremely high survival of young sea stars, and the industry was unable to cope with this added predation, even with the relatively successful control measures that it had developed previously. Recovery has been slow because many other natural and man-made problems exist, including oyster drills (*Urosalpinx cinerea*, and to a lesser extent *Eupleura caudata*), unpredictable effects of storms, and a highly variable and reduced supply of young oysters. Wallace (1971) has cited water pollution as one of the major problems of the oyster industry in New York, but he voiced great hopes for hatcheries, four of which now are producing seed in New York. By 1970 oyster production in the State had increased fivefold, but still only to about half a million pounds of meats (230 metric tons). Time will tell whether hatcheries are the answer to the problems of the industry. The idea certainly is not new. The first oyster hatchery in New York was in operation in 1921 (New York Conservation Department, 1969). MacKenzie (1970) has suggested that natural setting is adequate to supply the needs of the industry for seed, if adequate measures are taken to eliminate mortality from siltation, predators, and careless handling. The feasibility of these methods of rehabilitating the oyster industry, no matter how valid they may be biologically, needs to be tested by economic studies.

SOFT CLAM

Traditionally a popular seafood in New England and the middle Atlantic region, the soft clam (*Mya arenaria*) has produced steadily decreasing landings in New York (Figure 5). Production in 1880 was reported as more than 3 million pounds of meats (1,370 metric tons). Average annual landings for years on record from 1887 to 1908 inclusive were just under 1 million pounds

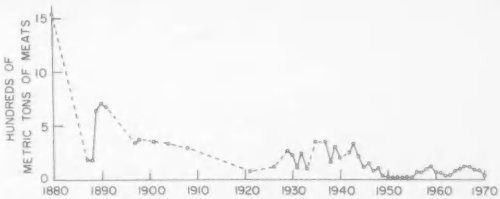

FIGURE 5.—Annual commercial landings of soft clam in the State of New York, 1880-1970.

(450 metric tons), from 1921 to 1945 inclusive less than half a million (200 metric tons), and from 1946 to 1970 less than 200,000 pounds (90 metric tons). To some extent the decline may have been caused by the long-term rise in water temperatures which in New England led to increased predation by green crabs. Wallace (1971) has attributed the decline in production to "pollution and physical changes in the estuaries." The soft clam is a vulnerable, shallow water species, and there is little doubt that overharvesting and lack of adequate regulation of the fishery were important factors.

BLUE CRAB

In the waters of New York State the blue crab, *Callinectes sapidus*, is near the northern limit of its range. It has never been a major species in the catch in this area. Because the blue crab is highly variable in abundance from natural causes even in the center of its range (McHugh, 1969a), it might be expected to be extremely variable in New York waters, and the history of the commercial fishery suggests that this has been true (Figure 6). Landings have declined steadily, but irregularly, since the maximum recorded catch of about 1.6 million pounds (725 metric tons) in 1880. Catches rose briefly in the 1930s, to a recorded peak of more than half a million pounds (270 metric tons) in 1935, but after a minor upsurdge in the early 1950s the fishery collapsed. No commercial catch has been recorded since 1961.

In Chesapeake Bay, with major fluctuations, the blue crab catch has been increasing for about 35 years. It has been suggested that the increased catch has been caused by increased

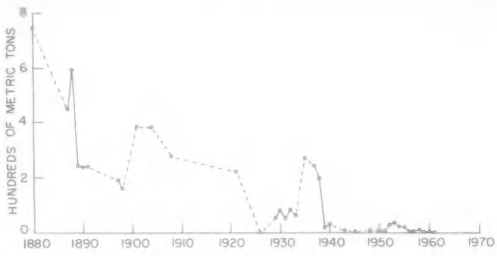

FIGURE 6.—Annual commercial landings of blue crab in the State of New York, 1880-1970.

abundance generated by nutrient enrichment in the estuaries (McHugh, 1969a), as was suggested also for striped bass (Mansueti, 1961). There is no direct evidence to support this hypothesis, but it is not untenable. Other than the decade of increased landings of blue crab which began about 1929 in New York, and a longer period of highly variable but substantially increased catches in the middle Atlantic region which ended in the late 1950s (McHugh, 1971),[3] there has been no similar continuing upward trend in blue crab production north of Chesapeake Bay. It is interesting to speculate that the enrichment of coastal waters and estuaries in the middle Atlantic region of the United States from domestic and industrial wastes may have stimulated blue crab production for a while, then became a limiting factor as eutrophication proceeded too far.

SHAD

The anadromous American shad (*Alosa sapidissima*), like the salmon, was a popular fish with the early settlers, wherever it was found along the Atlantic coast. Large catches have been reported in the early days from all major river systems. The Hudson River was one of the major producers, and maximum landings on record in New York State were more than 4 million pounds (2,000 metric tons) in 1889 (Figure 7). From 1880 to 1901 inclusive the average annual catch was over 3 million pounds (1,400 metric tons); from 1904 to 1935 inclusive it was only about one-tenth of this; then the catch began a steady rise to a peak of almost 3 million pounds (1,300 metric tons) in 1945, followed by an abrupt decline to less than a million pounds (275 metric tons) in 1949. Shad landings in New York for the last 3 years have been very much less than 100,000 pounds (about 16.5 metric tons).

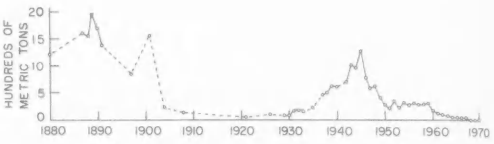

FIGURE 7.—Annual commercial landings of shad in the State of New York, 1880-1970.

This continued decline to what amounts to virtual collapse of the fishery is disturbing, especially in the light of the following statement by the Biological Section of the Scientific Committee of the Atlantic States Marine Fisheries Commission (1958a): "The Hudson River investigation has been completed and the fishery can now be managed successfully." What has gone wrong in little more than a decade?

The report cited above, and another special publication of the Atlantic States Marine Fisheries Commission (1958b) completely ignored the sharp increase in shad landings in New York, and indeed in the entire middle Atlantic region including Chesapeake Bay. At the time these reports were prepared the shad fishery of this entire region had swung from a maximum catch of nearly 36 million pounds (16,250 metric tons) in 1897 to a low of 5 million (2,270 metric tons) in 1935, to a secondary peak of about 12 million pounds (5,500 metric tons) in 1944 and again in 1945, and down again to less than 6 million pounds (2,700 metric tons) in 1958. It is difficult to reconcile the pompous statement quoted above with the past and subsequent history of the fishery (Figure 7). It is especially embarrassing to this author, who was chairman of the committee that issued these two reports.

[3] McHugh, J. L. 1971. Domestic wrangles and international tangles—the fisheries of the Middle Atlantic Bight. Unpublished manuscript, 237 p., filed at Woodrow Wilson International Center for Scholars, Washington, D.C.

The phenomenon of the rise and fall of the shad fishery in the Hudson River from 1924 to 1953 has been analyzed in some detail by Burdick (1954). He concluded that overfishing from 1941 to 1951 was responsible for the decline, which first became noticeable in 1946. He found no evidence that water pollution had any different effect on the shad stocks of the river during the period of rising catches than during the period after 1945. The overfishing was caused, according to Burdick, by the increased demand for fishery products during the war which led to relaxation of the fishing regulations (substantial shortening of the weekly closed season).

BLUEFISH

The bluefish (*Pomatomus saltatrix*) is a mysterious oceanic visitor to the coastal waters of New York. Commercial landings at the turn of the century (Figure 8) were 10 million pounds or more (average of about 4,800 metric tons for the 3 years 1897, 1901, and 1904). Early in the 20th century commercial landings dropped

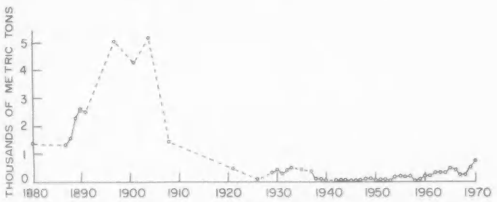

FIGURE 8.—Annual commercial landings of bluefish in the State of New York, 1880-1970.

abruptly, then rose from much less than a million pounds (135 metric tons) in the 1920s to about a million pounds (450 metric tons) in the 1930s, dropped to a very low level in 1940, and have been increasing, with some fluctuation, to nearly 2 million pounds (725 metric tons) in 1970.

Bluefish are an important and much sought after sport fish in the middle Atlantic region. Recreational catches for New York waters alone are not available in published analyses of data gathered by the Census Bureau (Deuel and Clark, 1968), but for the Atlantic coast as a whole the sport catch in 1965 was reported to be over 90 million pounds (41,000 metric tons), almost 15 times the total commercial catch of bluefish. Thus, it is probable that recreational fishermen take much more bluefish than commercial fishermen from New York waters. Briggs (1962, 1965, 1968) has confirmed that bluefish are among the most important species in the sport fisheries of Long Island.

Bluefish migrate to New York coastal waters in summer. Abundance is notably variable, but it is not understood clearly whether this is caused by real variations in abundance, or by a response to changing oceanographic conditions, or both. Abundance appears to have been increasing for the past 10 years or more.

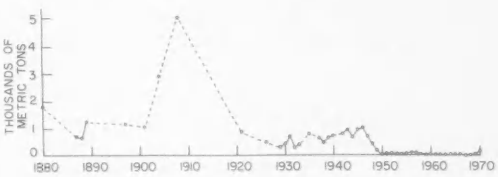

FIGURE 9.—Annual commercial landings of weakfish in the State of New York, 1880-1970.

WEAKFISH

The weakfish or gray seatrout (*Cynoscion regalis*) has been an important commercial species along the Atlantic coast. At the turn of the century most of the catch came from New York and New Jersey waters. Later the center of the fishery shifted southward to the area from Delaware Bay to the North Carolina sounds. The greatest landings recorded in New York were in 1908 (Figure 9) at over 11 million pounds (5,100 metric tons). Landings dropped to less than 1 million pounds (400 metric tons) in 1929, rose slowly to over 2 million (1,000 metric tons) in 1946, then dropped to very low levels after about 1948. The abundance of the species has declined along the entire Atlantic coast if commercial catches are a valid criterion. Recently, however, it apparently has been more abundant in the coastal waters of New York, especially in sport

fish catches. According to Perlmutter, Miller, and Poole (1956) weakfish available to New York fishermen belong to two distinct stocks, those which spawn locally and those which are southern spawned. These authors said that weakfish are abundant off New York only when the southern stock is large.

The recreational catch of weakfish in 1965 was estimated to be only 178,000 pounds (81 metric tons). It probably was considerably greater than this in 1970, but it appears that this is primarily a commercial species still.

The reason for the great decline in catches of weakfish is not known. Off Virginia in 1936 it was about 10 times as abundant as it was in 1946, according to the catch rate in pound nets (McHugh and Bailey, 1957). The increased catches in New York in the 1940s probably were caused by the increased demand for fish during the war, as already mentioned for several other species. Weakfish have been taken by trawlers in relatively deep water in winter, but the species has not been recorded in foreign catches off the Atlantic coast. Large numbers of young fish are killed by shrimp trawls in the Carolinas and in pound nets in Chesapeake Bay. Some people believe that this attrition has been responsible for the decline, but this source of mortality must have declined with the decline of the Atlantic coast pound net and shrimp fisheries.

SEA MUSSEL

Mussels are not in great demand as human food in the United States. Landings in New York State have been relatively small, seldom exceeding 1 million pounds of meats (500 metric tons). In 1908, however, a catch of over 8 million pounds of meats (3,800 metric tons) was reported, and in the 1940s (Figure 10) landings increased for a few years, probably because mussels were valued as a source of Vitamin D during the second world war. This may be a valuable latent resource if markets can be developed. The possibilities for aquaculture also should be investigated. Very high yields have been reported with hanging culture of mussels in Europe.

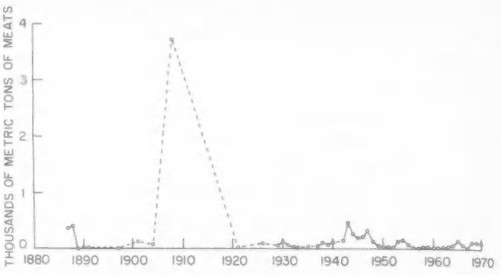

FIGURE 10.—Annual commercial landings of sea mussels in the State of New York, 1887-1970.

BAY SCALLOP

Bay scallop are in great demand and bring a high price. Landings in New York sometimes exceeded 1 million pounds of meats (520 metric tons in 1921) prior to 1932 (Figure 11), but the catch dropped sharply thereafter. The decline has been attributed to destruction of eelgrass

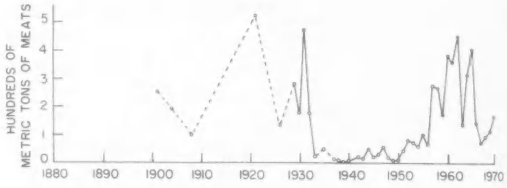

FIGURE 11.—Annual commercial landings of bay scallop in the State of New York, 1901-1970.

(*Zostera*) beds, by disease (*Labyrinthula*). As the eelgrass recovered, bay scallop became more abundant; and by 1962, landings in New York were up almost to a million pounds again. The abrupt decline to a low in 1967 may have been caused by overfishing.

HADDOCK

Haddock landings in New York apparently were at their greatest from 1908 to 1929 (Figure 12). The largest landing on record was in 1926 at about 17 million pounds (7,700 metric

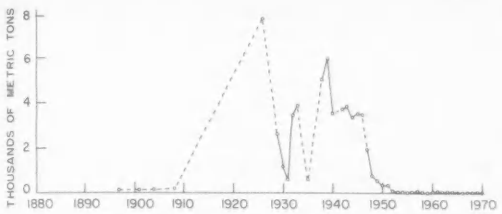

FIGURE 12.—Annual commercial landings of haddock in the State of New York, 1897-1970.

tons). Following a substantial drop in the 1930s the catch reached a secondary maximum in 1939, dropped to an average annual catch of about 8 million pounds (3,600 metric tons), to 1946 inclusive, then declined sharply, and remained extremely low for the last two decades. This decline of local haddock landings probably came about through the general decline of the New York trawl fleet after the war, for landings in New England, mostly from Georges Bank, remained remarkably steady from the late 1930s to the middle 1960s (Graham, 1968). Recent overfishing has brought the Georges Bank haddock stock to a very low level (Edwards, 1968), and it is unlikely that haddock will again become an important component of New York landings for some time, if ever.

TILEFISH

No record of tilefish (*Lopholatilus chamaeleonticeps*) landings in New York is available prior to 1929 in statistics published by the Federal Government. Yet Bigelow and Schroeder (1953) stated that 11,641,500 pounds (5,285 metric tons) of this species were caught off New England from July 1, 1916, to July 1, 1917. These authors concluded that the drop to less than half a million pounds (220 metric tons) in 1947 (about 42% of it in New York) was caused by a lack of demand.

The tilefish is of special interest to ecologists, although now a minor commercial species, because it inhabits a narrow band of ocean bottom at the edge of the continental shelf from Nova Scotia to southern Florida and in the Gulf of Mexico. Off New England and the middle Atlantic coast it is restricted to a zone of relatively warm water of about 8° to 12°C at depths of 82 to 360 m. Within 3 years after its existence was discovered in 1879 almost due east of New York Bight, the tilefish resource suffered a mass mortality. Large numbers of dead tilefish were reported floating at the surface over the edge of the continental shelf from off Delaware Bay to New England. The kill was attributed by Bigelow and Schroeder (1953) to a sudden shift or dissolution of this warm intrusion. The reduction in abundance was so drastic that no tilefish was taken in the area until 1892, and substantial commercial fishing on the resource did not resume until 1898. It is thus established that the tilefish is subject to very wide fluctuations in abundance from natural causes.

When tilefish first appeared in the commercial fishery statistics for New York State in 1929, landings were about 2.5 million pounds (1,180 metric tons). The catch fluctuated between 1 million (454 metric tons) and 2.5 million pounds in the period 1929 to 1935, then dropped sharply to nearly zero in the middle 1940s (Figure 13).

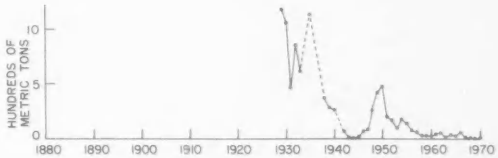

FIGURE 13.—Annual commercial landings of tilefish in the State of New York, 1929-1970.

A secondary maximum of just over a million pounds was reached in 1950, and subsequently landings in New York dropped steadily to a very low level. The collapse of this fishery in New York may have been caused by lack of demand, by the general decline of the trawl fisheries of the State after the war, by a natural decline in abundance, or by overfishing. Tilefish are not listed separately in the statistical bulletins of ICNAF, but are included under "other groundfish." In 1968 this category included a catch of 172,000 metric tons of mixed fish, which

could have included significant quantities of tilefish. A deep-sea sport fishery has developed recently (Richard H. Schaefer, personal communication).

COD

Cod, like many of the species caught principally or exclusively in otter trawls, was landed in maximum quantities in New York 30 to 35 years ago (Figure 14). The peak catch was about 8.5 million pounds (3,870 metric tons) in 1938, and landings declined sharply thereafter, as the trawl fishery of the State declined. The trend of New York landings of cod prior to 1940 was different from the trend of total U.S. catches of the species, which have declined irregularly since the last decade of the 19th century from 60,000 metric tons to less than 12,000 metric tons in 1953 (Graham, 1970). After 1940, cod landings in New York dropped at a fairly steady rate, from about 3 million pounds (1,450 metric tons) to less than half a million (200 metric tons) in 1970.

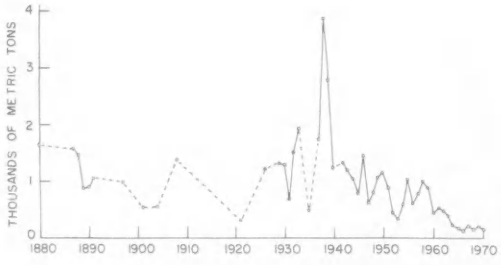

FIGURE 14.—Annual commercial landings of cod in the State of New York, 1880-1970.

The cod resource of the North Atlantic Ocean is tremendous, as demonstrated by the dominance of this species in landings from the ICNAF regulatory area. In 1968, for example, the catch of cod in this area was 1.86 million metric tons, about 48% of the total catch of all species from the area, which included at least 120 species of fish, shellfish, and other marine organisms of commercial value. Neither Graham (1968) nor Edwards (1968) considered that the cod stocks in the areas fished by Americans were overexploited. Edwards (1968) estimated that the standing crop in those areas was about 489 million pounds (222,000 metric tons), of which about 32% was being caught annually. Nevertheless, according to ICNAF annual reports pressure on the cod stocks is heavy, and there is some evidence that yields could be increased by increasing the mesh size of the trawls.

Cod is not the principal species sought by the U.S. fishing fleet but is taken incidental to the haddock fishery. A substantial sport fishery for cod has developed along the north and middle Atlantic coasts of the United States. The recreational catch in 1965 was estimated to be nearly 30 million pounds (13,580 metric tons).

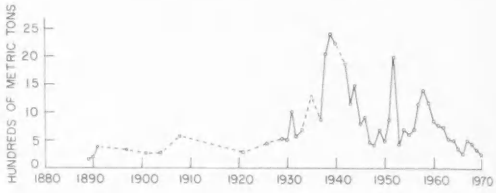

FIGURE 15.—Annual commercial landings of butterfish in the State of New York, 1889-1970.

BUTTERFISH

The trend in landings of butterfish in New York (Figure 15) is not unlike the pattern for cod (Figure 14) and other trawl-caught species. The maximum catch was more than 5 million pounds (2,380 metric tons) in 1939. Thereafter, the catch declined irregularly to a low of about half a million pounds (240 metric tons) in 1970. The pronounced variations in catch were probably caused mainly by variations in success of spawning. The downward trend reflects the decline of the trawl fishery. Small panfishes like butterfish, which cannot be filleted and made into fish sticks or portions at reasonable cost, have declined in popularity as the frozen fish industry has developed. Reduced demand for such kinds of fish almost certainly has contributed to the decline of the New York trawl fisheries.

Relatively large quantities of butterfish are taken by foreign fishing fleets in international waters. In 1968 the total reported catch in the ICNAF statistical area was about 4,000 metric tons, somewhat less than half of which was caught by American fishermen. New York's share was only about 10% of the domestic catch.

Edwards (1968) estimated that the standing crop of butterfish off New England and New York was about 309 million pounds (140,300 metric tons) of which only about 3% is taken each year by the commercial fisheries. He considered that the resource is underutilized, mainly because it is a midwater species for which no effective fishing gear has yet been developed.

Schaefer (1967), sampling with a beach seine in the surf along the south shore of Long Island, found that butterfish were the most abundant species in his catches in 1961. In 1962 and 1963 they dropped to third and sixth place respectively, which may mean that this species varies widely in abundance from natural causes.

There is no recorded sport catch of butterfish, although it is known that they will bite on small baited hooks.

SILVER HAKE

Silver hake, often called whiting, is the most abundant groundfish on New England banks according to Edwards (1968). Demand for silver hake as a food fish is limited in the United States. Much of the domestic catch is used for animal food, and some as industrial fish. Edwards (1968) estimated that the standing crop on American fishing grounds in the middle 1960s was about 2.1 billion pounds (nearly a million metric tons) and that the average annual catch by all commercial fishing fleets was about 31% of the standing crop. Peak landings in New York were about 6 million pounds (2,690 metric tons) in 1943 (Figure 16). The catch declined to an average of less than a million pounds (420 metric tons) from 1948 to 1952, then rose and maintained an average annual level of about 2.8 million pounds (1,270 metric tons) for 16 years, from 1954 to 1969 inclusive. In 1962 foreign catches began to rise rapidly from previously

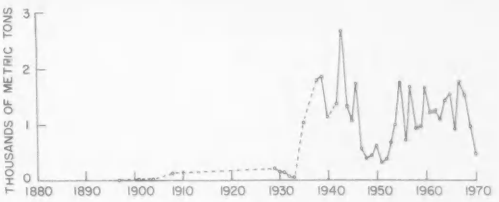

FIGURE 16.—Annual commercial landings of silver hake in the State of New York, 1897-1970.

low levels. The total catch in the ICNAF area reached 373,000 metric tons in 1965, then dropped just as abruptly, but New York landings were not affected very much, nor were U.S. landings as a whole. Strong year classes apparently were produced in 1967 and 1968, which augurs well for the fishery in 1970 to 1972 (International Commission for the Northwest Atlantic Fisheries, 1969). The recent decline in New York landings can be attributed only to the decline of the local trawl fleet.

The sport catch of silver hake in the New England and middle Atlantic areas in 1965 was estimated to be about 6 million pounds (2,720 metric tons).

NORTHERN PUFFER

The northern puffer, or swellfish, although it is abundant from Cape Cod southward, was not considered to be an important food fish until meat rationing during the second world war stimulated the coastal fisheries. The greatest catch in New York waters was in 1945, when almost 2.5 million pounds (1,060 metric tons) were landed. Subsequently the catch declined to less than 200,000 pounds or about 70 metric tons (Figure 17), rose to a secondary maximum in 1963 (nearly a million pounds or 430 metric

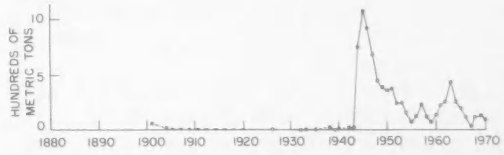

FIGURE 17.—Annual commercial landings of northern puffer in the State of New York, 1901-1970.

tons), and dropped off again. Until recently most of the catch has come from Gardiners and Peconic Bays; but as landings dropped in the middle 1960s, fishing effort shifted to the ocean off the south shore of Long Island and to a lesser extent into Long Island Sound.

Richard Miller, Executive Secretary of the Long Island Fishermen's Association (personal communication), says that the decline in New York landings of northern puffer was caused by the growing fishery in Chesapeake Bay (McHugh, 1969a), which led to a substantial decline in prices.

The declining catch of northern puffer in the bays of the eastern end of Long Island may have been caused by the decline of the pound net fishery, by overfishing, or by natural causes. The drop has been substantial, from a maximum of over 850,000 pounds (385 metric tons) in 1963 (over 90% of total commercial landings of puffers in New York) to 90,000 pounds (41 metric tons) in 1969 (less than 35% of total New York puffer landings). Recent development of fisheries for this species in the ocean and in Long Island Sound suggest that it may be generally an underexploited resource in the waters of the State.

The northern puffer is one of the more important species in the coastal sport fisheries of New York, although this is more by accident than by design. According to Briggs (1965) they are regarded as a nuisance, especially by flounder fishermen, who complain that puffers "steal their bait." Indeed, when puffers are abundant in Great South Bay, spring catches of winter flounders go down, not necessarily because they are less abundant but because puffers take the bait more readily and this discourages flounder fishermen. In the bays of eastern Long Island the catch of puffers by sport fishermen apparently has not had a great effect on the commercial fishery, for Briggs (1968) found that this was not a particularly important element of sport catches there.

The increase in commercial landings of puffers from 1960 to 1963 (Figure 17) probably was caused by a real increase in abundance. This is confirmed by two sport fishing studies. Briggs (1965) estimated that the sport catch of puffers in Great South Bay increased about fivefold from 1960 to 1962, from about 58,000 to about 314,000 fish. The sport catch was almost as high in 1963 as in 1962. Schaefer (1967) estimated the relative abundance of fishes in the surf zone on the south shore of Long Island and found that puffers were the most abundant species in catches of a beach seine in 1962 and 1963 (about two-thirds of all the fish caught), whereas in 1961 less than 1% of the catch had been puffers.

In 1965 it was estimated that about 26 million pounds (11,750 metric tons) of northern puffers were taken by sport fishermen along the middle Atlantic coast.

ATLANTIC MACKEREL

Once an important fishery, the domestic Atlantic mackerel industry has been producing for the last 15 years or more only about 3% of the maximum recorded catch in 1884 (Hoy and Clark, 1967). Landings of mackerel in New York have fluctuated more or less in proportion to domestic landings along the Atlantic coast as a whole. Most of the catch in New York now is made in pound nets, although gill nets at one time were the most important gear. Thus, to some extent the decline in New York landings (Figure 18) may have been caused by the decline of the pound net fishery. The demand for mackerel in the United States also is less than it was early in the century. Abundance varies widely from natural causes (Sette, 1938).

FIGURE 18.—Annual commercial landings of Atlantic mackerel in the State of New York, 1887-1970.

Mackerel are important in high-seas fisheries by foreign fleets. In 1968 the total catch reported from ICNAF statistical areas was 71,595 metric tons, of which only 3,001 metric tons were caught by American commercial fishermen. Thus, the present total catch by all nations is almost equal to the greatest domestic catch on

record. The estimated recreational catch in 1965 was nearly 19 million pounds (8,590 metric tons). It appears that the decline of the domestic mackerel fishery was a matter of declining demand and that sport fishermen and foreign fleets have willingly preempted the harvest.

Edwards (1968) noted that mackerel have not been abundant in the northwestern Atlantic recently, but that abundance has been increasing.

SEA BASS

Landings of sea bass in New York fluctuated around a level of about half a million pounds (225 metric tons) a year until 1943 (Figure 19), when the catch began to rise sharply, reaching a maximum of about 2.8 million pounds (1,270 metric tons) in 1951. Then the annual landings began to drop just as sharply, and they are still falling. Commercial landings in New York in 1970 were only about 70,000 pounds (32 metric tons). This is primarily a fish of shallow waters,

FIGURE 19.—Annual commercial landings of sea bass in the State of New York, 1887-1970.

and no landings have been reported by foreign fleets in the ICNAF statistical areas. Sea bass move offshore to deeper water in winter, and some may be included in the unidentified category. Most of the domestic commercial landings in New York are caught in otter trawls, and a substantial part of this sea bass catch comes from outside the 3-mile limit, if not beyond the zone of domestic fishery jurisdiction.

For the Atlantic coast as a whole the recreational catch of sea bass in 1965 was estimated to be nearly 11 million pounds (4,945 metric tons), more than 2.5 times the total commercial catch on the Atlantic coast in 1970. Partial surveys of the sport fisheries of Long Island, cited elsewhere, do not show that this is a very important recreational resource in this area.

The decline in sea bass landings in New York is attributable at least partly to the decline of the trawl and pound net fisheries. Landings in New Jersey and the Chesapeake Bay States have declined also, but neither as abruptly nor as soon. It is not known whether the resource has been overfished, and it appears that to some extent the decline in commercial landings may have been offset by increased recreational catches.

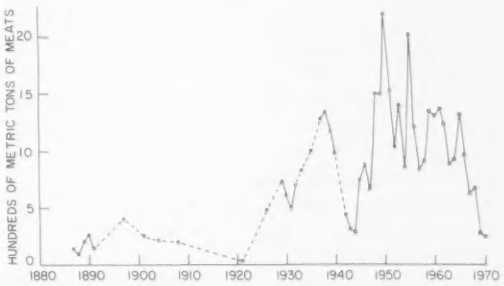

FIGURE 20.—Annual commercial landings of sea scallop in the State of New York, 1887-1970.

SEA SCALLOP

The history of sea scallop landings in New York has been generally similar to the history of landings of the same species in New England (Graham, 1968). The recent sharp decline in New York landings (Figure 20) has the same causes as the similar decline of the U.S. sea scallop catch as a whole: increased catches by foreign fishermen, and generally poor survival after the last highly successful spawning which reinforced the scallop population on Georges Bank early in the 1960s. Sea scallop landings at Fulton Fish Market declined abruptly after 1965, and by 1970 the number of trips by scallop dredgers landing their catch there had dropped considerably.

SCUP

As illustrated by Figure 21, scup became increasingly important in New York landings in the 1940s and 1950s, reaching a maximum of

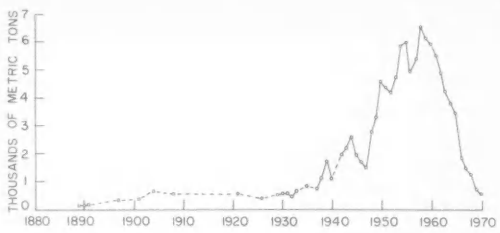

FIGURE 21.—Annual commercial landings of scup in the State of New York, 1889-1970.

over 14 million pounds (6,490 metric tons) in 1958. In fact, scup ranked first by weight of all food fishes and shellfish landed in New York from 1953 to 1961 inclusive. The subsequent decline was abrupt, the catch dropping to just over a million pounds (545 metric tons) in 1970. Almost all of the catch was made by otter trawls, most of it beyond the 3-mile limit, and about half of it landed at Fulton Market in New York City. The causes of declining commercial catches are not understood at all clearly. The total domestic catch in 1970 was only about 10.5 million pounds (4,770 metric tons), less than what was landed in New York alone in 1958. The foreign catch in 1968 was only about 5 million pounds (2,255 metric tons). The total recreational catch in 1965 was estimated to be about 37.6 million pounds (17,075 metric tons).

Briggs (1968) found that scup were the most important species by numbers caught in the sport fisheries in the bays of eastern Long Island. In 1965, for example, he estimated that the total catch in this small area was over a million fish, 44% of the catch by numbers. The following year the sport catch in the same area was reduced by nearly 50%. Finkelstein (1969) noted that from historical times scup were known to go through extreme variations in abundance, from great abundance to such scarcity that the species was virtually absent for years.

Edwards (1968) estimated that the standing crop of scup from New York Bight north was about 66 million pounds (30,000 metric tons) per year from 1963 to 1965. Average annual commercial landings in the same period were about 10 million pounds (4,540 metric tons), and thus the commercial fisheries were taking only about 15% of the standing crop each year. It would appear from all these estimates and other data that if the decline in scup landings has been caused by fishing, the sport fisheries have been the principal contributing agent. However, it appears equally likely that variations in spawning success could be the cause. Of course, when the resource is at an extremely low level of abundance, whatever the cause, it may be much more vulnerable to heavy fishing intensity.

FLOUNDERS

The major species of flounder in the New York catch are yellowtail, winter flounder or blackback, and summer flounder or fluke. Other names which appear in United States or ICNAF statistics are gray sole (*Glyptocephalus cynoglossus*), which ICNAF calls witch; lemon sole, which is simply a winter flounder that weighs more than 3½ lb. (1.6 kg); dab (*Hippoglossoides platessoides*) which is called American plaice by ICNAF; and hogchoker (*Trinectes maculatus*). The last two, and perhaps some other species, may be included under unidentified categories in New York landings. This vernacular and scientific terminology is so confusing that these names have been listed and properly paired off in Table 2 as compared with the official listing of the American Fisheries Society (Bailey, 1970).

Individual species of flounder were not identi-

TABLE 2.—Common and scientific names of flounders as used in domestic (NMFS) and international (ICNAF) statistics, and as endorsed by the American Fisheries Society (AFS).

Common name	Source	Scientific name
Yellowtail flounder	NMFS, ICNAF, AFS	*Limanda ferruginea*
Blackback flounder Lemon sole Winter flounder	NMFS (under 3½ lb.) NMFS (over 3½ lb.) ICNAF, AFS	*Pseudopleuronectes americanus*
Fluke Summer flounder	NMFS ICNAF, AFS	*Paralichthys dentatus*
Gray sole Witch Witch flounder	NMFS ICNAF AFS	*Glyptocephalus cynoglossus*
Dab American plaice	NMFS ICNAF, AFS	*Hippoglossoides platessoides*
Hogchoker	NMFS, ICNAF, AFS	*Trinectes maculatus*

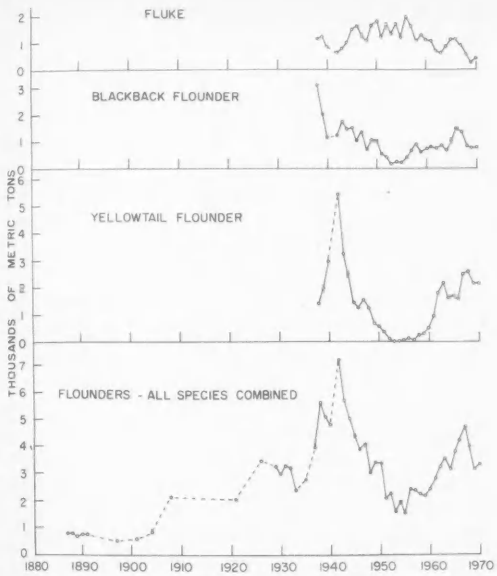

FIGURE 22.—Annual commercial landings of flounders in the State of New York, 1887-1970.

fied in U.S. statistics until about 1938 (Figure 22). Total landings of all flounder species in New York have two maxima, one at nearly 16 million pounds (7,130 metric tons) in 1942 and the other at more than 10 million (4,720 metric tons) in 1967. Between these peaks the catch dropped off to an average annual minimum level of about 4 million pounds (1,850 metric tons) from 1951 to 1955 inclusive.

Most of this dip, and much of the subsequent rise, was caused by a wide oscillation in landings of yellowtail flounder (Figure 22) from about 12 million pounds (5,400 metric tons) in 1942 to virtually nothing in 1952 to 1957, then back to nearly 6 million pounds (2,565 metric tons) in 1968. Graham (1968) attributed these fluctuations to changes in abundance of yellowtail flounder, without citing causes. Royce, Buller, and Premetz (1959) went into the question in detail. Edwards (1968) estimated that the standing crop of yellowtail flounder in areas fished by Americans was 185 million pounds (84,000 metric tons). Average total landings from these same areas from 1963 to 1965 were more than 50% of the standing crop annually, which is the highest fishing rate for any species in the area.

Smith (1963, 1968, 1969) also noted the increasing abundance of yellowtail flounder in the 1960s on grounds frequented by New York fishermen. Despite an abrupt drop in numbers of trawlers landing their catches at Fulton Fish Market in New York City from 1960 to 1966 (a drop of approximately 80%) the weight of yellowtail landed nearly doubled. From 1960 to 1965 and 1966 the catch of yellowtail per trip rose from about 71 lb. to about 700 lb., a crude but fairly convincing index of increasing abundance. Lux (1969) presented evidence that dominant year classes spawned in 1958, 1959, and 1960 produced greater abundance of yellowtail on fishing grounds off New England from 1960 to 1963, but that abundance declined from 1964 to 1966. Alarmed at the heavy rate of fishing on this resource, ICNAF established catch quotas in 1970 aggregating 29,000 metric tons, and in the following year reduced this quota to 26,000 tons.

The yellowtail flounder is a species of relatively deep water. No catches were reported by sport fishermen in 1965.

Winter flounder landings in New York also declined from the 1930s to the early 1950s, then rose again. The domestic commercial catch dropped from nearly 7 million pounds (3,050 metric tons) in 1938 to about a third of a million (160 metric tons) in 1953, then back to slightly over 3 million (1,475 metric tons) in 1966. According to Poole (1969) winter flounders have been abundant recently in New York waters. He attributed the relatively small commercial landings in the State to restrictions on trawling which have been in effect for 25 to 30 years. This is primarily a fish of shallow coastal waters. In 1968 in the western North Atlantic foreign fleets took only 1,200 metric tons, as compared with a total domestic commercial catch of about 10,700 metric tons.

The total U.S. sport catch of winter flounder in 1965 was nearly 29 million pounds (over 13,000 metric tons). The species is important in the saltwater sport fisheries of the State.

Briggs (1962, 1965, 1968) found that about 1.5 million fish were taken in Great South Bay each year and about another million per year in Moriches, Shinnecock, Gardiners, and Peconic Bays. In 1964 to 1966 he found that winter flounders made up from 17 to 40% of the sport catch by numbers in the bays of eastern Long Island.

Edwards (1968) estimated that the standing crop of winter flounder in the northwestern Atlantic was about 185 million pounds (84,000 metric tons), about the same as the estimate for yellowtail. The rate of exploitation by commercial fleets, however, was considerably less, about 17% per year.

Commercial landings of summer flounders in New York (Figure 22) have followed essentially the same trend as commercial catches for the New England and middle Atlantic States as a whole, reaching a maximum in the 1950s and dropping off fairly steadily thereafter. Poole (1966) suggested that the increase in catch from 1938 to the 1950s was a result of increased fishing effort, not increased abundance. Commercial landings in New York are only about 20% of total commercial landings, and there is no reported foreign catch. The total recreational catch in 1965 was estimated to be nearly 35 million pounds (15,800 metric tons), about 6 times the total commercial catch of 5.7 million pounds (2,590 metric tons).

The summer flounder, like the winter flounder, is one of the most important sport fishes in New York waters. Briggs (1962) found that from 1956 to 1960 sport fishermen took about 1.5 million fish per year from Great South Bay alone. The New York State Department of Environmental Conservation has estimated that 1.7 million anglers fish each year in marine waters of the State (A. C. Jensen, personal communication). Their removals of summer flounder and other species are a very important part of total fishing mortality.

SURF CLAM

The surf clam fishery of the Atlantic coast began its period of major growth in the middle 1940s. Landings in New York (Figure 23)

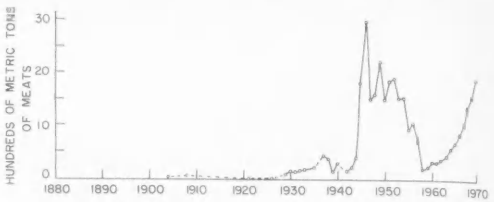

FIGURE 23.—Annual commercial landings of surf clam in the State of New York, 1904-1970.

were relatively small compared with New Jersey, which reached a level of over 43 million pounds (19,600 metric tons) of meats in the late 1960s. But the fishery began off Long Island and shifted south later, as abundance dropped on local beds. The resurgence of the New York surf clam industry after 1958 came about through discovery of new offshore beds and development of more efficient harvesting gear. The future of the surf clam fishery of the State is uncertain because, like all molluscan shellfish resources, this species is extremely vulnerable to overharvesting, and controls are difficult to impose. The history of our shellfisheries is a history of overexploitation, and there is no reason to believe that the surf clam industry will be any exception. This industry grew because the soft clam and oyster industries inshore were declining. The great demand for clams and the current high prices will be great incentives to harvest known resources heavily and to seek out new grounds.

HARD CLAM

In landed value hard clams have been the most important commercial fishery species in New York since 1953. Landings reached a maximum in 1947 of nearly 11 million pounds (4,700 metric tons) of meats, then dropped abruptly to 1954 (Figure 24). Since the middle 1950s landings have climbed steadily from a low of about 2.5 million pounds (1,100 metric tons) in 1954 to nearly 8 million (3,590 metric tons) in 1970. Most of this increase has come from Great South Bay, which in 1959 produced about 1.5 million pounds (680 metric tons) of meats and in 1969 yielded more than 6 million pounds (2,860 met-

ric tons). This almost doubled the percentage contribution of Great South Bay to the total hard clam production of the State.

In discussing this growth of the hard clam industry in New York, Wallace (1971) pointed out that hard clams are much more adjustable to changing environmental conditions than oysters are, even in the larval stages. In Raritan Bay, once the center of oyster production in the area of New York Bight, hard clams still spawn successfully, although much of the bay is badly polluted and oysters are long since gone. He attributed the great rise in hard clam production in New York to a series of excellent sets in several bays on the south shore of Long Island.

FIGURE 24.—Annual commercial landings of hard clam in the State of New York, 1880-1970.

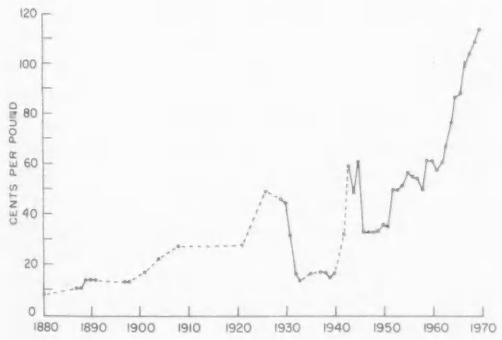

FIGURE 25.—Average annual landed value of hard clam meats in the State of New York, 1880-1970.

It would appear that part of the incentive to harvest clams more intensively has been provided by economic changes. As Figure 25 illustrates, the landed price per pound of hard clam meats has undergone some interesting changes over the years. Prices were high in the affluent days before the depression of the 1930s. In the 1930s they dropped to what probably would be a record low if the figures had been expressed in standard dollars. Prices rose sharply during the war and dropped as sharply immediately afterwards, as did the prices of most seafoods. Then in the 1950s the price of hard clams began to rise and the rise continued even more rapidly in the 1960s. This steady increase over a period of two decades can be explained only partially by the declining value of the dollar. The economic forces operating here must be largely if not completely the collapse of the oyster and soft clam industries and the growing affluence of most segments of the population, which seems always to stimulate demand for the more popular kinds of seafood, especially invertebrates.

STRIPED BASS

Commercial landings of striped bass (*Morone saxatilis*) in New York have been following an upward trend for the past 30 years or more (Figure 26). The same phenomenon has been observed along the Atlantic coast from Chesapeake Bay (McHugh, 1969a) north. The total Atlantic coast commercial catch in 1970 was about 10.5 million pounds (4,770 metric tons). The total

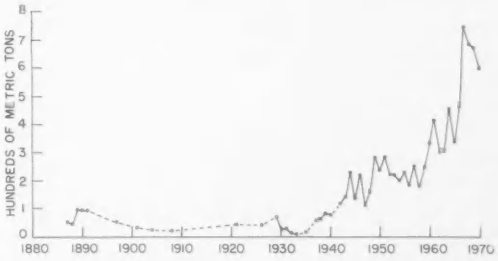

FIGURE 26.—Annual commercial landings of striped bass in the State of New York, 1887-1970.

estimated sport catch in 1965 for the Atlantic coast was between 5 and 6 times the weight of the commercial catch in 1970. The striped bass is an anadromous coastal species, and it has not been reported in catches of foreign fleets fishing offshore.

It seems unlikely that the great increase in striped bass landings over a 35-year period has come about through an equivalent increase in fishing effort, for this species has been popular as a commercial and recreational species for a long time. It has been suggested (Mansueti, 1961) that the species has been able to take advantage of increased nutrient loads in its nursery areas in Chesapeake Bay and elsewhere and that the increased catch has been largely, if not completely, caused by a real increase in abundance. This is entirely hypothesis, and data probably do not exist with which to test it. A small piece of suggestive evidence on a closely related species has been published recently. Tsai (1970), examining changes in fish stocks of the Little Patuxent River, Md., over a period of about a decade, found that some species had decreased considerably in abundance and others had increased. Among the species which had increased was the semi-anadromous white perch (*Morone americana*), which has a life history very similar to that of the striped bass during the first 2 years of its life when it does not move very far from the influence of the river in which it was born.

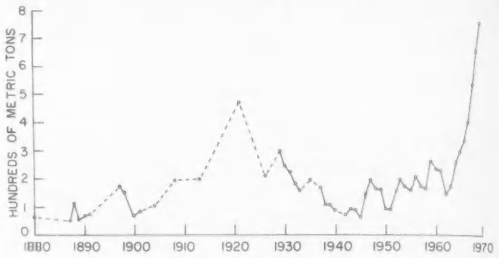

FIGURE 27.—Annual commercial landings of northern lobster in the State of New York, 1880-1970.

NORTHERN LOBSTER

Landings of lobster in New York also have been increasing for about 25 years. The maximum catch recorded in the earlier period was a little over a million pounds (470 metric tons) in 1921 (Figure 27). Then the catch fell off rather steadily to a low of about 150,000 pounds (64 metric tons) in 1945. In 1970 about 1.65 million pounds (750 metric tons) were landed in New York. The recent increase has been attributed to two phenomena. The first has been a general decline in coastal water temperatures for the last 10 years, which apparently has brought about a southward shift in the distribution of lobster and an increase in pot catches inshore. The second has been the increasing exploitation of hitherto unused lobster resources by trawls and pots in relatively deep water on the continental shelf. Graham (1968) stated that several inshore species along the Atlantic coast, including lobster, were producing catches at or beyond levels of maximum sustainable yield and that from now on the fluctuations in annual landings would be the result of fluctuations in recruitment or availability. The relation between the offshore and inshore lobster stocks is not completely understood, but recent investigations seem to be leading to the conclusion that the offshore lobster fishery may be harvesting a distinct stock. If so, it cannot yet be determined how large a catch it can sustain. The future of lobster landings in New York would appear at this time to be uncertain.

CONCLUSIONS

Consideration of trends in landings of some 28 species of marine fish and shellfish in the State of New York shows that the variable commercial fishery production of the State has been maintained by shifting from one species or stock to another as landings of each resource have risen to maxima and then declined, often to very low levels. The reasons for some of these declines or increases are known, but trends in landings of many species remain unexplained. At any point in time in the history of the coastal fisheries of New York, landings of some species are rising, and others declining, and there is no reason to believe that the pattern will change.

Even if a constituency receptive to rational management of the fisheries could be created, only a few of these resources are subject to control unilaterally by the State of New York. Most would require cooperative effort by all States through the waters of which the living resources migrate. Such cooperation has not been possible, although a mechanism exists in the Atlantic States Marine Fisheries Commission to provide cooperative management, if cooperation is really desired. To date, the Commission has demonstrated neither the desire nor the capability for joint management of coastal fishery resources.

In New York it can be expected that the situation may deteriorate further. Since 1962 the total weight of fish and shellfish landed in the State has dropped from more than 112,000 metric tons to about 14,500 metric tons, a decline of about 86% in 8 years. Most of this decline has been in the industrial fisheries, principally menhaden, but food fish landings have dropped also. Over the same period food fish and shellfish landings have dropped from about 18,000 metric tons to about 14,500 metric tons, a decline of about 21%. Indeed, the trend in seafood production has been downward for more than 30 years. Since 1938 New York seafood landings have dropped about 54% from 31,100 metric tons.

The species have been discussed approximately in chronological order of maximum commercial catch. This sequence was chosen because it illustrates rather nicely some of the reasons for the fluctuations observed. The sequence of rise and decline is typical of the evolution of coastal fisheries. Note that the first eight species of food fish and shellfish discussed, with two exceptions, are either molluscan shellfish or relatively nonmigratory species of shallow coastal waters, or anadromous. The two exceptions, bluefish and weakfish, although highly migratory, crowd into coastal bays and estuaries seasonally, where they are highly vulnerable to fishing. These are the kinds of fish and shellfish that support the early fisheries everywhere. They can be taken easily with primitive gear, sometimes without even the aid of a boat, and thus they are extremely vulnerable. To this group can be added menhaden and river herrings.

The next 12 species or groups of species, with only one exception, can be placed in two general categories: fish which come into coastal waters in abundance at times, but which also are abundant offshore; and those which seldom, if ever, come into coastal waters. Among these are demersal species like haddock and tilefish, densely schooling and highly migratory pelagic fishes like mackerel, or mollusks of relatively deep waters like sea scallop or surf clam. Many of these are taken by trawls, dredges, or purse seines, which require relatively large, powered vessels. This requires more capital investment and more manpower, hence calls for more organization and planning. These are the kinds of fish and shellfish to which coastal fishermen turn when the strictly coastal resources no longer can meet market demands. This is the typical evolutionary pattern of coastal fisheries, in which the fleets expand, increase in efficiency, and range out into the ocean and farther from their home bases. Almost all of these fisheries now are declining.

The one exception noted above is the northern puffer or swellfish, which as far as we know is very much a species of the coastal zone, living in shallow waters near shore. As such, it might be expected that the northern puffer fishery would have developed and declined much earlier than it did. The reason probably is that puffers have been regarded as repulsive, and their value as a first-class food fish was not recognized until recently. The well-known toxicity of tropical puffers also may have been a contributing factor.

The last three species discussed—northern lobster, striped bass, and hard clam—interestingly enough, are essentially resources of the coastal zone, which, like the puffer, would be expected to be subject to heavy fishing early, hence produce maximum landings early and then decline. Under most circumstances this might have been so, but special circumstances apply to each. With the lobster it is a matter of increasing availability in New York coastal waters in re-

sponse to natural environmental change and a new offshore lobster fishery on previously unexploited stocks. With striped bass it has been speculated that man-made changes in the environment actually have caused substantial increases in abundance. The recent increase in hard clam production may have a similar cause, but economic factors may also have played a part.

These trends and their relationships can be visualized more clearly by grouping species with more or less similar chronological patterns of landings (Figure 28). The seven groupings here illustrated were derived according to the decade in which the maximum catch was reached. The result forms almost a "textbook example" of the evolution and decline of a regional fishery.

Although the causes of most short-term changes in the landings are complex, the long-term deterioration of certain formerly important fisheries leads to the uncomfortable conclusion that lack of management and overfishing probably are important causes. The oyster, once by far the most important seafood resource in New York by weight or by landed value, today no longer ranks among the 10 most important species. Menhaden, an industrial fish, once the dominant species in New York landings by weight, and far outweighing all other species combined, today ranks eighth by weight, and the industry on which it was based is close to collapse. The oyster catch has been largely a cultivated crop, and in New York the efficiency of cultivation has been superior to that in any area except the Pacific Northwest. The recent decline of the industry has been caused by natural disasters with which the industry was unable to cope. But many of the problems could have been avoided by applying knowledge of the ecology of oysters, according to MacKenzie (1970), and the potential yield is far greater than the industry has ever realized. In other

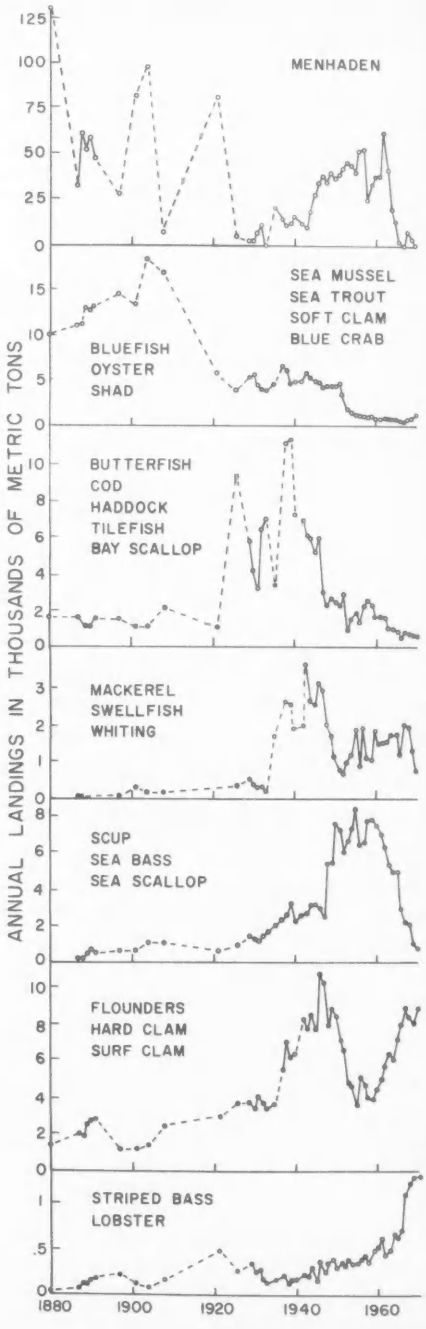

FIGURE 28.—Annual commercial landings of fish and shellfish in the State of New York, 1880-1970. The species have been grouped according to the decade in which the greatest landings were made and the groups are arranged approximately in chronological order of maximum landings. The two peaks in the second graph from the bottom do not represent a shift from one species to another. See text for details.

words, MacKenzie has said that although the methods used by oyster planters in New York were relatively efficient as compared with methods employed in most other parts of the country, they could have been much better, and rehabilitation is possible. This conclusion may be challenged by oystermen, for the studies on which it is based did not consider adequately the economics of oyster planting.

The second most important food fish of the early days was the shad, entirely a wild crop. This fishery has declined just as sharply as the oyster fishery, and the causes are entirely by man: deterioration of the environment in the rivers where spawning takes place and the young live their early lives, overfishing, and lack of effective management measures. The decline of the menhaden industry also can be attributed to overfishing, but in this case in areas to the south, not under the control of the State of New York.

The prospect is bleak. The history of the fisheries of New York, as in so many other coastal States, is a history of mismanagement, or perhaps more accurately a classic example of no effective management at all. As in other coastal States, there has been no dearth of attention to the matter by the public and by government. The laws of New York State include many limitations upon fishing and upon degradation of the aquatic environment, but the history of the fisheries does not attest that these laws have been effective. Perhaps the best that can be said is that if there had been no laws, the decline probably would have been more rapid and more severe.

Two solutions to these problems are popular today. The first begins with the premise that all the problems of the domestic commercial fisheries are caused by foreign fishermen. The proposed solution is that the United States should assume ownership, or at least trusteeship, over the fishery resources of the continental shelf by extending its zone of jurisdiction unilaterally to 200 miles, as several Latin American countries have done. It is argued that the matter is urgent and that we cannot afford to wait for international action at the Law of the Sea Conference in 1973. Supporters of this view, who include most, if not all, people in the fishing industry on the Atlantic coast, believe that nothing useful to them is likely to emerge from the 1973 conference, if indeed any agreement on fisheries is reached, or if the conference materializes at all. Meanwhile, if we take no action, they argue, the situation will deteriorate rapidly.

This argument is open to question for several reasons. Not the least of these is the sorry history of our own attempts to manage the living resources of coastal waters over which we have always had control. This has been demonstrated very clearly for the coastal waters of New York in the present paper, and the record of most of our maritime States is equally bad. Only when we have been compelled to do so under international agreements, as in the salmon fisheries of the Pacific coast, has the United States succeeded in managing any major coastal fishery. If we move unilaterally to extend our fishery jurisdiction, there is nothing in the record to demonstrate that this will amount to anything but a hunting license to destroy the living resources of a much broader zone of the sea.

The second popular solution arises out of the long standing controversy between recreational and commercial fishermen. Most saltwater sport fishermen probably would support a move to extend the width of the fishery zone. In addition, they would welcome restrictions of various kinds on domestic commercial fishermen, on the grounds that the commercial fisheries take large quantities of fish which are more valuable as recreational resources, or that commercial fishermen destroy the food supply or the spawning grounds of recreational species. These tend to be emotional issues in which facts are ignored or distorted and uninformed opinions prevail. Where the sport catch has been demonstrated to exceed the commercial catch greatly, as is apparently true for species like bluefish and striped bass, the question arises whether sport fishing is not more in need of regulation than commercial fishing. The growing sport fisheries are under much less control than the commercial fisheries are, but from a scientific point of view they are equally in need of control if management is to succeed.

SOME QUESTIONS FOR CONSIDERATION

This preliminary study will be the first step in developing a marine fishery program in the State University of New York. The program will be developed in coordination with plans and programs of appropriate State and Federal agencies and other institutions concerned, to complement rather than to duplicate. The university has valuable skills and facilities for investigating aspects of the fisheries that government is not investigating or cannot do. Some of the questions are:

1. Which living resources are amenable to management by the State; and which are not, without cooperation from others?
2. What are the potential benefits of investing public funds in fishery research and management? Are they being realized now? Are they worth pursuing? What should be the priorities?
3. What are the present and potential economic values of marine commercial and recreational fisheries in the State? On what basis should the resources be allocated among users?
4. Can the present alarming trends in the marine fisheries of the State be arrested, and the fisheries stabilized for maximum (or optimum) yield? What will it cost? What benefits will accrue?
5. Does marine aquaculture hold promise for the economy of the State? In what ways? What are the priorities?
6. How can the university best use its capabilities for public education and extension services to create an enlightened constituency for utilization and management of the living resources of the sea?
7. What is the policy of the State toward fishery research, development, and management? Is it a rational policy? Is it working? If not, what should the policy be and how should it be implemented?

These are but a few of the questions that need to be answered, and which the State University is well qualified to answer. They will require the attention of many disciplines, including economics, sociology, government, law, and international affairs, as well as the natural sciences. This historical review has helped to phrase the questions, but it has answered few. It is just the beginning.

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SPACE SCALES OF SEA-SURFACE TEMPERATURE PATTERNS AND THEIR CAUSES

JEROME NAMIAS[1]

ABSTRACT

The space scales of monthly mean sea-surface-temperature (SST) anomalies over the North Pacific are determined from data gathered over a 20-year period and analyzed with the help of correlation fields. The characteristic scales are ascribed to complex coupling between the atmosphere and ocean—specifically to long waves in the upper westerlies and latitudinal variations in the westerlies, both of which produce anomalous oceanic advection and heat exchange. The coherence of mid-tropospheric (700-mb) heights, the cross-correlations between these and SST values, plus atmospheric "teleconnections" (long distance relationships) implicit in these upper-level flow patterns reveal the character of coupling.

At the historic 1958 CalCOFI meetings at Rancho Santa Fe the central theme was the large-scale climatic warming of the North and equatorial Pacific which had evolved over a few years preceding the conference (Sette and Isaacs, 1960). Elton Sette, who co-chaired this meeting, stimulated much discussion of the time and space scales of this warming. In his work over subsequent years he has made numerous major contributions to the subject of large-scale oceanic temperature patterns. It is the purpose of this note to bring to light some new data and ideas relevant to these problems and thus serve both as a testimonial to Elton's work and as an expression of gratitude for his unceasing encouragement to those of us working along similar lines.

The source of data for the present work is a series of monthly mean sea-surface temperatures (SST) extending from 1947 to 1966 generated at the Scripps Institution of Oceanography from files of about 8,000,000 ship reports which were compiled by the National Marine Fisheries Service from the National Weather Service reports. Monthly averages of 2° geographic squares were computed and then further averaged around 5° intersections for areas north of lat 20°N. A 20-year average for each month was then computed. Departures of the monthly means from the 20-year averages were used in the work described below along with 700-mb heights obtained directly from the National Weather Service.

To determine the coherence of North Pacific SST patterns and possible teleconnections between them I have correlated the SST deviations from the 20-year mean at one point with deviations of the other 154 points used in the 5° oceanic grid for each of the winter months (December, January, and February) over the 20-year period making a set of 60 values for each point. Examples are shown in the middle charts of Figures 1, 2, and 3. A similar procedure was used with the atmospheric 700-mb heights as shown in the upper charts of these figures. Finally, cross-correlation fields were prepared relating SST point values to the 700 mb-height values elsewhere as shown in the lower charts. The latter two sets of charts involving atmospheric parameters were constructed to help explain the physical nature of the large-scale air-sea coupling which accounts for the observed scale of the predominant SST patterns.

Before discussing these charts, I should mention that the 700-mb level rather than sea level

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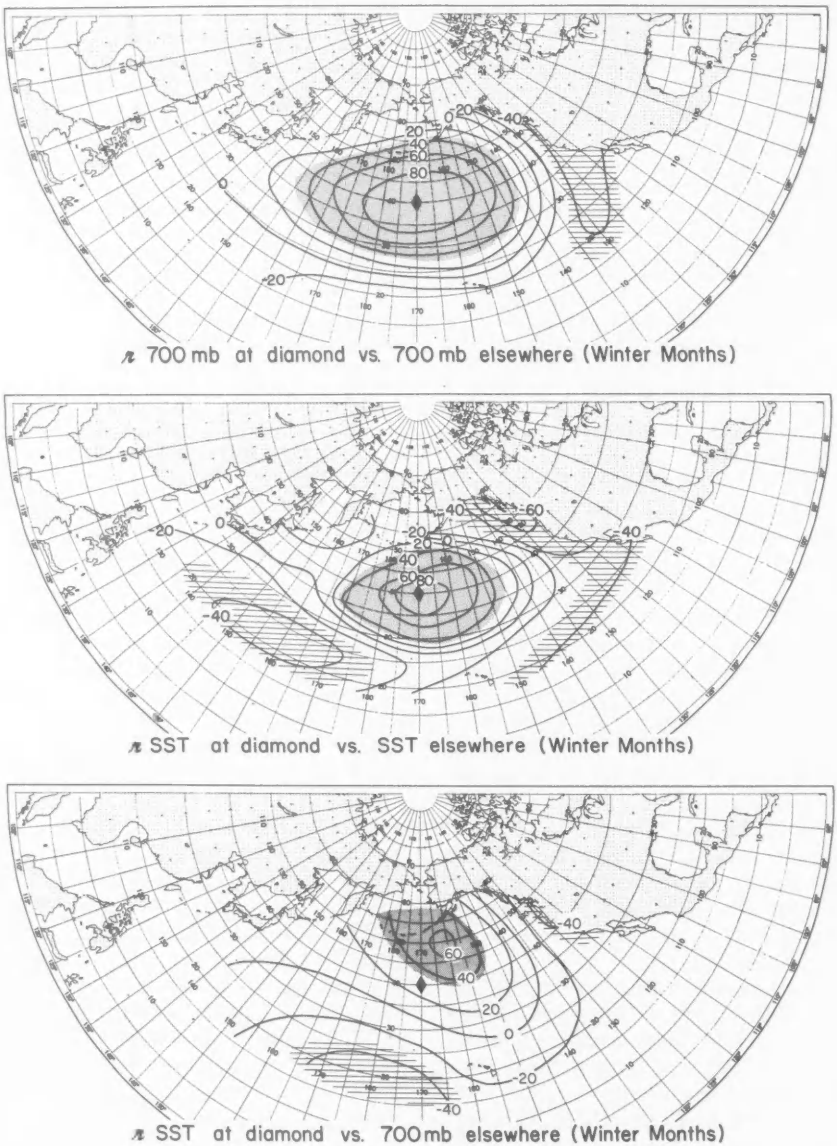
r 700 mb at diamond vs. 700 mb elsewhere (Winter Months)
r SST at diamond vs. SST elsewhere (Winter Months)
r SST at diamond vs. 700 mb elsewhere (Winter Months)

FIGURE 1.—Contemporaneous correlations between lat 40°N, long 170°W (diamond) and elsewhere for 700-mb heights (upper), sea-surface temperatures (middle), and SST vs. 700-mb (lower). Shaded areas represent correlations exceeding 1% level of significance—positive correlations stippled, negative hatched.

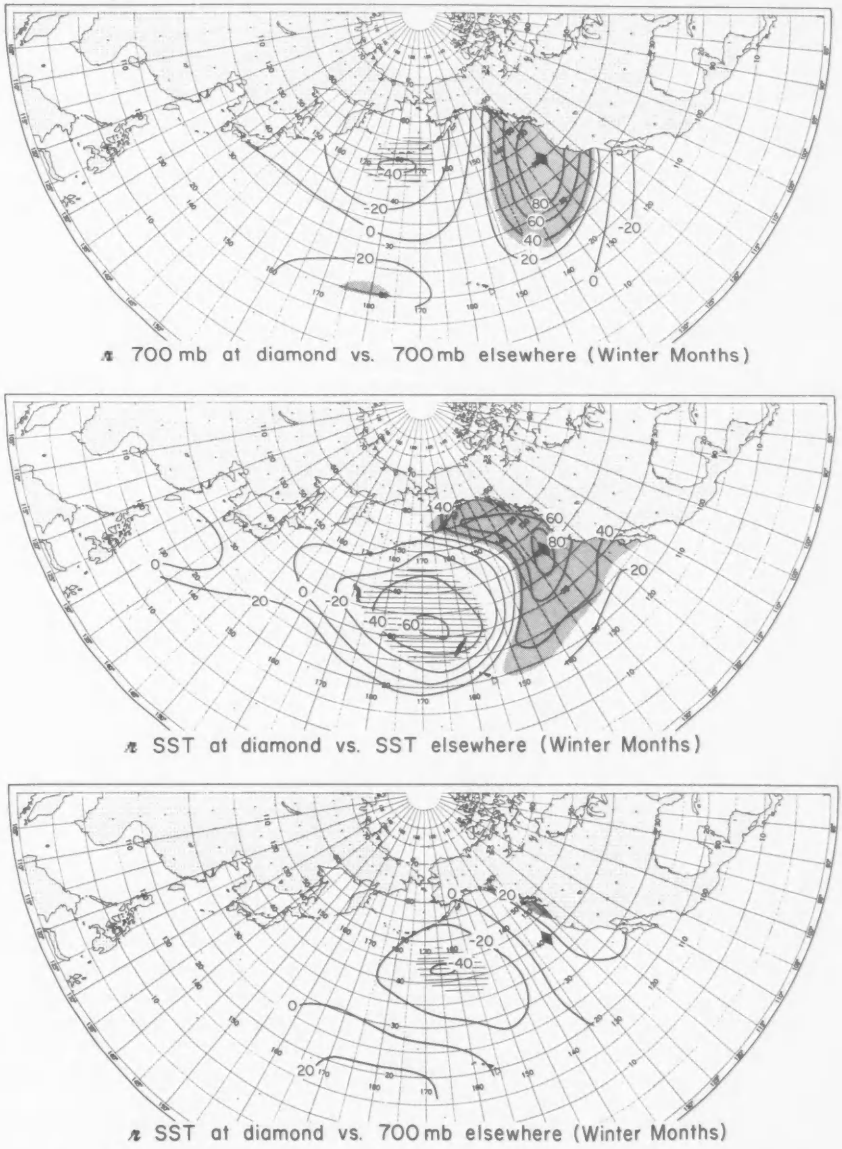
r 700 mb at diamond vs. 700 mb elsewhere (Winter Months)
r SST at diamond vs. SST elsewhere (Winter Months)
r SST at diamond vs. 700 mb elsewhere (Winter Months)

FIGURE 2.—Contemporaneous correlations between lat 40°N, long 130°W (diamond) and elsewhere for 700-mb heights (upper), sea-surface temperatures (middle), and SST vs. 700-mb (lower). Shaded areas represent correlations exceeding 1% level of significance—positive correlations stippled, negative hatched.

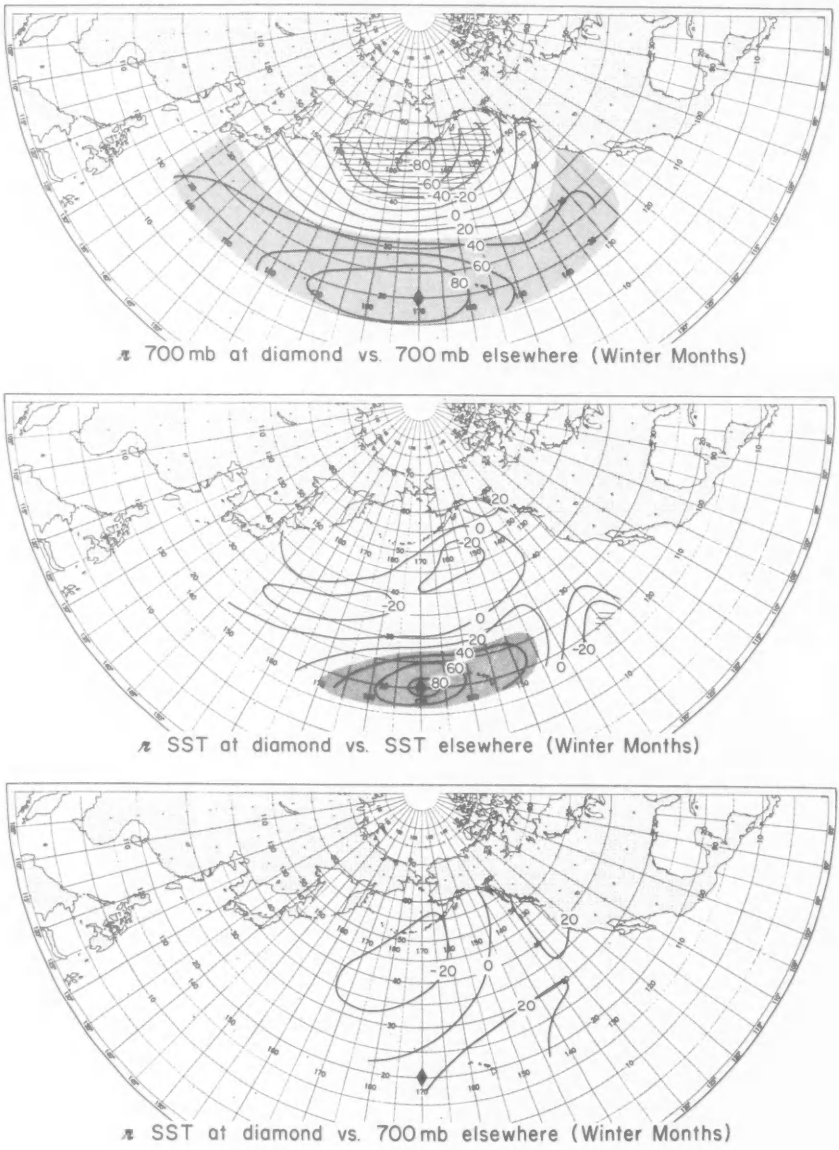
r 700 mb at diamond vs. 700 mb elsewhere (Winter Months)
r SST at diamond vs. SST elsewhere (Winter Months)
r SST at diamond vs. 700 mb elsewhere (Winter Months)

FIGURE 3.—Contemporaneous correlations between lat 20°N, long 170°W (diamond) and elsewhere for 700-mb heights (upper), sea-surface temperatures (middle), and SST vs. 700-mb (lower). Shaded areas represent correlations exceeding 1% level of significance—positive correlations stippled, negative hatched.

was chosen for the atmospheric variable because mid-tropospheric wind patterns often give a better specification of contemporaneous SST patterns than do sea-level maps. In general terms the physical reasons underlying this better specification from 700-mb rather than sea-level patterns lie in the fact that the 700-mb anomalies reflect not only the character of the anomalous sea-level pressure and wind distribution but they also contain implicitly the vertical stability of the lower troposphere. This association results from the high positive correlation between 700-mb height and mid-tropospheric temperature, and with cyclonic or anticyclonic contour curvature (Namias, 1947). The stability of the 1,000-700-mb layer to a large extent determines the vertical heat, moisture, and momentum flux from the surface—fluxes which are naturally important factors entering into the heat budget of the sea. Furthermore, since 700-mb height usually implies 700-mb temperature over ocean areas, some rough measure of back radiation is implied by the 700-mb heights.

Returning now to Figures 1-3 several points clearly emerge:

1. The space scale of coherent SST anomaly patterns is large—perhaps of the order of one-fourth to one-third of the North Pacific.

2. The SST scales are not far different from the 700-mb height scales and indeed display a remarkably similar form.

3. Strong teleconnections exist between SST anomaly fields of opposite sign over areas spanning almost one-half of the North Pacific; these teleconnections appear to be related to similar 700-mb teleconnections.

To aid the explanation of the above three empirical findings it should be remembered that time-averaged atmospheric patterns over large areas in temperate latitudes always reveal the presence of long or planetary waves whose horizontal dimensions are about 4,000 miles from crest to crest, but whose geographical positioning varies from month to month and also between the same month of different years. Thus, the atmospheric anomalies (and resultant prevailing winds and air masses) also vary. A quasi-stationary anomalous wind pattern generally creates anomalous SST patterns of a certain form. Most often cold water is advected and appreciable heat extracted in the cold dry northerly air currents behind mid-tropospheric troughs, while warmer water masses are advected and less heat extracted in the warm moist air currents ahead of troughs. Therefore, with atmospheric long-wave dimensions such as 4,000 miles (crest-to-crest) it is not surprising to find in Figure 1 that both 700-mb heights and SST anomalies are *negatively* correlated between the Central Pacific and the West Coast of the United States (one-half wave length) while both have similar coherence fields around the diamond.

Further clarification of the physical mechanism for this coupling can be obtained from the cross-correlations of SST with 700-mb height (Figure 1, lower). With anomalously warm water in the Central Pacific there are apt to be high 700-mb heights (anticyclonic ridge) in the north but low heights (cyclonic trough) in the south. Since correlation fields of the type shown in the upper and lower portions of Figures 1 and 3 may be interpreted in terms of flow (Stidd, 1954), we can approximate the resultant wind by remembering that it flows parallel to the contours with lower heights to the left. The anomalous wind component at the diamond is thus southeasterly and leads to less loss of heat by evaporation and sensible heat and greater advection of warm water from the south. Note also the contemporary reaction to *northerly* anomalous wind components in the eastern North Pacific—accounting for the colder than normal waters usually found there when the diamond area is warm. Of course, the above reasoning may also be applied (in reverse sense) when anomalously cold water exists at the diamond.

Figure 2, relating surrounding values to the diamond at lat 40°N, long 130°W, also shows the large-scale coherence and area of negative correlation one-half wave length upstream. The isopleths in the bottom figure indicate warm southerly air flow and warm sea transport accompanying positive SST values at the diamond and negative 700-mb height departures from normal in the Central Pacific. Of course, abnormally low SST values at the diamond imply

anomalous cold air and sea advection from the north.

Figure 3, which relates surrounding values to the diamond at lat 20°N, long 170°W, instead of demonstrating the east-west (trough-ridge) teleconnections described in connection with Figures 1 and 2, focuses on north-south teleconnections. These relationships were first pointed out by Walker and Bliss (1930) in studies of the North Pacific Oscillation, and later expanded by Willett, Bodurtha, and staff (1949),[2] Lorenz (1951), and O'Connor (1969). The upper section of Figure 2 shows that 700-mb heights are strongly negatively correlated between lat 20°N and 50°N, implying a north-south half-wave length of some 30° latitude.

A large part of this negative correlation is associated with "blocking" situations (low zonal index patterns) wherein anticyclones are found near the Aleutians contemporaneously with cyclones near Hawaii (Kona Storms). In the reverse case, abnormally strong Aleutian Lows are usually accompanied by strong subtropic anticyclones (high zonal index patterns).

The middle portion of Figure 3, while showing large-scale coherence around the diamond, indicates that the area of negative correlation lies farther south in the SST pattern than in the 700-mb pattern, so that little correlation exists between SST anomalies at lat 50°N and lat 20°N in the central North Pacific. Probably this small degree of correlation implies a much more complex mechanism than wind-driven advection and heat exchange, or that sea-level anomalies in these situations are not well prescribed by the 700-mb anomalies. Also, the diamond lies outside the zone of major influence of the westerlies.

Although there is a strong tendency for North Pacific SST anomaly patterns to have compensating large pools of warm and cold water, it should not be assumed that the mean temperature anomaly of the entire North Pacific is zero. Figure 4 shows that the mean SST for the entire

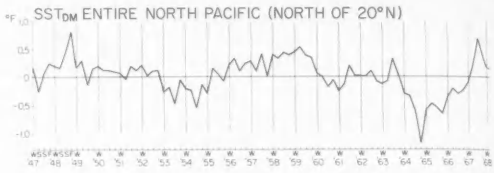

FIGURE 4.—Departures of mean sea-surface temperature (°F) from the 1947-66 averages over the entire North Pacific, north of lat 20°N.

North Pacific (north of lat 20°N) varies over a range of about 2°F in extreme seasons, and as much as 1°F in extreme *years*! Assuming normal atmospheric parameters, a 1°F change would imply a difference in heat of evaporation of 47.8 $\times 10^{20}$ cal., equivalent to the evaporation of 8.14 $\times 10^{18}$ g of water or about 23.4 cm of water over the entire North Pacific. The oceanic mean SST anomalies are highly correlated with the area occupied by positive signs of the SST anomalies ($r = 0.84$). Thus, the North Pacific mean anomaly is often determined not by the domination of some extreme values but by the vast extent of major anomalous areas. For example, during the extreme negative SST anomaly of fall 1964 and extreme positive anomaly of summer 1967 (see Figure 4) 14% and 73% respectively of the North Pacific had positive signs. Large areal anomalies of this sort arise from the fact that the sea has a much greater persistence than the atmosphere (Namias and Born, 1970). Hence, large warm or cold pools in one area, such as the western Pacific, are apt to resist rapid change over a month or even a season, while the eastern Pacific may be undergoing more rapid response. This differential rate of response may be due to a more shallow thermocline in one area of the Pacific than another and/or more vigorous atmospheric circulation changes.

These almost ocean-wide extremes of SST are naturally transitory, because their space scale is not compatible with modal long-wave atmospheric patterns, so that ultimately compatible patterns must be restored.

The high positive correlation between mean SST over the entire North Pacific and percent of the total area occupied by positive signs may

[2] Willett, H. C., F. T. Bodurtha, and Staff. 1949. Final report of the Weather Bureau - M.I.T. extended forecasting project for the fiscal year July 1, 1948-June 30, 1949. Mass. Inst. Technol., Cambridge, Mass., 109 p. ("Memorandum of Understanding" with the U.S. Weather Bureau.) [Processed.]

TABLE 1.—Correlation relating mean SST over North Pacific (north of lat 20°N) and percent of positive signs of anomalies at 5° squares (based on 21 years of data), and standard deviations of these quantities.

	Correlation $\overline{SST}$ vs. % positive anomalies	σ $\overline{SST}$ (°F)	σ % of positive signs
Winter	0.83	0.28	9.77
Spring	0.71	0.25	9.20
Summer	0.87	0.37	14.18
Fall	0.86	0.40	14.21
All seasons (overall)	0.84	0.32	11.90

be found in all seasons with only small differences (see Table 1). However, the variability in percent of similar signs and mean SST seems to be seasonally dependent with summer and fall having greater variability than winter and spring, as shown by the standard deviations of SST and percent of positive signs listed in Table 1. In the warm season small changes in cloud cover and wind can produce large changes in SST since only a thin wind-mixed layer is affected. These changes often extend over vast areas because of variations in the great Pacific High and peripheral storm tracks.

ACKNOWLEDGMENTS

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MONTHLY SEA LEVEL DIFFERENCES BETWEEN THE HAWAIIAN ISLANDS AND THE CALIFORNIA COAST

J. F. T. SAUR[1]

ABSTRACT

Time series of monthly sea level differences, adjusted for linear trends and the isostatic effect of atmospheric pressure, are computed for Honolulu-minus-San Francisco (1905-69) and Hilo-minus-Avila (1947-59 and 1961-67) as an index to broad scale changes in current around the eastern limb of the North Pacific anticyclonic current gyre.

The normal seasonal cycle of sea level differences imply a net southeastward surface current that is strongest from April through October and weakest from December through February and the range is about 20% of the average. Nonseasonal differences for Honolulu-minus-San Francisco and Hilo-minus-Avila show a highly significant correlation over the 240 months of coincident records. Inferences regarding nonseasonal large-scale long-term changes in geostrophic current are drawn from the 65-year Honolulu-minus-San Francisco smoothed monthly anomalies in which variability of less than 6 months was suppressed, as follows: 1) nonseasonal changes in current speed exceed $\pm$ 10% of the normal current over one-third of the time and range up to 54% of the normal monthly current, 2) the periods 1922-38 and 1950-54 were eras of low variability as compared with greater variability in the rest of the record, and 3) periods of weakest circulation were in 1911, 1918, 1941, 1957-58, and 1967, and of strongest circulation in 1915, 1920-21, 1943-44, 1948-49, and 1959.

For more than a decade there has been a rapidly growing interest of fishery scientists and biological oceanographers in the role of the environment in fishery problems. One objective is to include environmental effects in models of population dynamics and in fishery forecasting procedures. However, to do this, environmental characteristics which are significant to fisheries must be determined and set forth in quantitative form. One empirical approach to these complex environmental problems is to compile historical oceanic and atmospheric data into time series to gain a knowledge of the mean seasonal cycles and variability, identify periods of highly anomalous environmental conditions for further study, and seek an understanding of cause-effect relations which bring about the observed changes. Such an understanding would be useful for efficient monitoring of the oceanic environment and in predicting environmental conditions.

Oceanographic data with good time and space distribution for time-series studies of environmental changes of a few months to several years are woefully scarce. Only sea-surface temperature observations taken by ships as a part of the marine weather observations have long-term continuity in time as well as oceanwide distribution. As a result, these have been used extensively in air-sea interaction studies and to indicate oceanic changes.

To augment the sea temperature data, mean sea levels compiled from continuous tidal records at coastal and island stations provide another source of long time-series data on ocean variability. The statistical characteristics and interrelations of the sea levels, atmospheric pressure, and temperature of many coastal and island stations in the Pacific have been described in several papers by Roden (1960, 1963, 1966) using autocorrelation, spectral, and coherence techniques.

[1] National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92037.

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The data have been less utilized in the study of specific oceanographic changes. Stewart, Zetler, and Taylor (1958) pointed out the rise in sea level along the west coast of North America during the warming period of 1957-58. Bjerknes (1966) also noted changes in sea levels along the equator during El Niño, i.e., warming which occurs off the Pacific coast of South America, during the same 1957-58 period.

In this paper the use of sea level information in the northeast Pacific Ocean to augment inferences about oceanographic changes is explored. The geostrophic equation requires that the speed of the surface current be proportional to the transverse slope of the sea surface. Thus time series of differences in sea level between the Hawaiian Islands and the California coast could be an index to broad-scale changes in surface current in the eastern North Pacific Ocean. Some earlier exploratory work on sea level differences between Honolulu and San Francisco through 1962 was reported orally at meetings of the American Geophysical Union (Saur, 1966). These preliminary results indicated that a pronounced weakening of the strength of the south flowing current around the eastern limb of the North Pacific current gyre was associated with the warm winters of 1940-41 and 1957-58, which have been reported for the California Current region (Reid, 1960; Robinson, 1961). The occurrence of El Niño in these same periods (Bjerknes, 1961, 1966) further indicated the possibility of a relaxation in strength of ocean current systems in the eastern Pacific on a broad scale.

No time series of direct observations of ocean conditions exist to study such broad-scale changes in current, and certainly not of the continuous nature of sea level data. In this paper therefore, the normal seasonal cycles of sea level differences between the Hawaiian Islands and the California coast are presented and some inferences are drawn from the 65-year record of Honolulu-minus-San Francisco differences about the character of changes of surface current in the region.

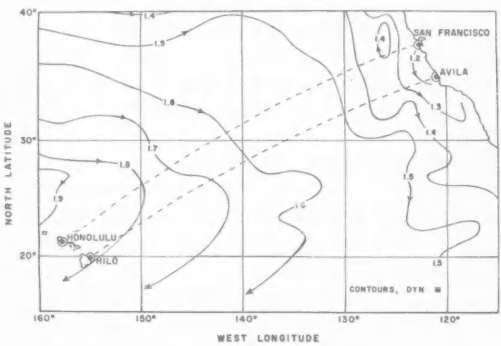

FIGURE 1.—Station locations and general pattern of surface currents (solid contours: geopotential anomaly at the sea surface relative to the 1,000 db surface, in dynamic meters) after the NORPAC Atlas (Oceanic Observations of the Pacific, 1960) but modified near the Hawaiian Islands per Reid (1961) and Seckel (1962). Dashed lines are great circles joining pairs of tide stations for which sea level differences are calculated.

EARLIER STUDIES

Montgomery (1938) was the first to use the cross-current difference in sea level in the geostrophic equation to estimate the range of fluctuation of ocean current. Using changes in sea level difference between Charleston, S.C., and Bermuda, he found the range of seasonal variation was about 32% of the average difference. Stommel (1953) used fluctuations in cross-current sea level differences between Havana and Key West and between Cat Key and Miami as a measure of current in developing a model of the structure of the Florida Current. More recently, Wunsch, Hansen, and Zetler (1969) measured statistical variability of the Florida Current by spectral and coherence analyses of longer sea level records at the same four stations. They found that the apparent seasonal variation of the Florida Current accounts for only about 10% of the root-mean-square modulations for periods from 2 days to 1 year. They further concluded that monthly mean sea levels could be used to indicate long-period fluctuations.

Changes in mean sea levels at shore stations have been favorably compared by other investigators with changes in geopotential height of the sea surface in deep water offshore as traditionally determined from observed subsurface distribution of density of the water column. Mont-

gomery (1938) cautioned that he had only a meager number of hydrographic stations for this, but other studies since that time tended to confirm his results.

For the southern California coast, LaFond (1939) found good agreement between weekly sea level and contours of dynamic height (0/500 db) extrapolated to the tide station. Special observations of sea level and temperature structure were carried out at many island stations during the International Geophysical Year from which Lisitzin and Pattullo (1961) concluded that in the open ocean most of the deviations from mean sea level can be explained by combined atmospheric pressure effects and steric effects, the latter being defined as those due to changes in the specific volume of the water column, i.e., those measured by dynamic height anomalies. Shaw and Donn (1964) had 173 hydrographic stations, taken approximately biweekly by the *Panulirus* off Bermuda over a period of nearly 7½ years, to compute steric levels for comparison with sea levels. They found that about 80% of the variance of raw sea levels, which included the seasonal cycle, resulted from a combination of the atmospheric pressure effect, which was weak, and the steric effect, which was dominant.

Sturges (1966) has shown high correlations between steric levels and mean sea level at two Pacific coast locations. The least squares regression of steric levels computed for the coast against 3-day sea level (adjusted for atmospheric pressure) for Neah Bay, Wash., was 0.97 with a standard error of estimate of 4.1 cm and a correlation of 0.904. The regression coefficient at San Diego, Calif., was only 0.61 with a standard error of estimate of 2.2 cm and a correlation of 0.914. Theoretically, for variations of sea level adjusted for pressure to agree with steric level, the slope of the regression should be unity. Sturges also estimated the wind set-up effect at Neah Bay, which has a narrow continental shelf, to be negligible.

Such studies indicate, as summarized by Donn, Pattullo, and Shaw (1964), that the combined atmospheric pressure and steric effects account for most of the sea level variations of periods longer than a few months. Thus, the interpretations made here assume that sea level differences, suitably adjusted for trends and atmospheric pressure, are a reasonable measure of changes in broad-scale geostrophic currents.

SURFACE CURRENTS OF THE REGION

Our area of interest is shown in Figure 1. Sea level differences between Honolulu and San Francisco and between Hilo and Avila are to be studied. The great circles joining each pair of stations span the same region of the eastern North Pacific Ocean.

The currents in the region are part of the eastern limb of the major anticyclonic current gyre of the North Pacific Ocean. The general pattern is shown in Figure 1 by the 0/1,000 db contours of dynamic height anomaly. The surface current is generally to the southeast, nearly normal to the great circles over most of the distance. At these latitudes the California Current extends from the California coast to about long 130°W, or somewhat farther, and about one-half of the change in geopotential anomaly takes place across this current, i.e., in less than one-third the distance between the stations. As a typical eastern boundary current (Wooster and Reid, 1963), it is broad, sluggish, and reinforced by coastal upwelling during the spring and summer months. During the winter months, December through February, a narrow north flowing countercurrent, often referred to as the Davidson Current, frequently occurs at the surface along the central California coast.

The California Current feeds into the North Equatorial Current, the axis of which lies south of lat 20°N (Seckel, 1962) so that there is generally a southward component across the great circle near the Hawaiian Islands. Occasionally, however, there is a west-northwestward flow along the east side of the islands, as evidently occurred at the time of the 1955 Norpac survey (Oceanic Observations of the Pacific, 1960). Corresponding to this return flow across the great circle, the sea levels at the Hawaiian stations would be lower than sea level northeast of the islands. Such localized conditions cannot be revealed by the sea level data, and thus are one source of "noise" in the data.

DATA AND PROCEDURES

Monthly mean sea levels were obtained from the National Ocean Survey[2] which has for many years compiled these data for its tide stations. The coincident period of record for Honolulu and San Francisco is 65 years, 1905-69. The coincident period for Hilo and Avila is 20 years, 1947-59 and 1961-67. It is broken and shortened because of incomplete records at Avila. However, Avila was selected among other California stations to pair with Hilo, so that the great circle between them would be close to that joining Honolulu and San Francisco and would cross essentially the same currents.

All of the tide gauges have moderately good exposure. Hilo and Avila are small coastal harbors protected by artificial breakwaters. The Honolulu gauge is in the outer of two harbor areas just inside of the entrance channel. The San Francisco gauge is at Fort Point just below the Golden Gate Bridge on the south side of the entrance to San Francisco Bay. Depths of 100 fm (183 m) are less than 10 km offshore from Hilo and Honolulu tide gauges, less than 20 km off Avila, and about 55 km off San Francisco.

ELIMINATION OF TRENDS

The sea level observations refer to the level of the ocean surface relative to the adjacent land. The annual mean sea levels at each of the four stations increase irregularly with time as shown in Figure 2. Such long-term trends as are due to a combination of change in the total mass of ocean water by melting (or accretion) of glaciers and of local subsidence (or emergence) of the land on which the gauge is located (Hicks and Shofnos, 1965), need to be eliminated from the data.

The linear trends determined by least squares regression, of 0.17 cm/year at Honolulu and 0.20 cm/year at San Francisco (Figure 2) are essentially the same as reported by Hicks and Shofnos (1965) for sea levels through 1962 at the same stations. The trend of 0.24 cm/year at Avila is only slightly larger than the first two, but the trend of 0.57 cm/year at Hilo is well over twice as large. In a computer analysis of the tide records at five stations in the Hawaiian Islands, Moore (1971) found a pattern of near zero trend at the older islands to the northwest increasing consistently toward the southeastern younger islands. Moore attributes the greater trend at Hilo to subsidence caused by loading of the crust by active volcanism. An interesting study by Apple and MacDonald (1966) of archeological features—native bait cups, net tanning tubs, and playing boards—carved into a newly submerged reef at Honaunau, Hawaii, further indicates a century of subsidence like that indicated by the recent tide gauge records.

By an indirect method using the decay constant of the autocorrelation coefficient Roden (1966) examined the consistency of trends for moving 30-year periods in the longer records at Honolulu and San Francisco. He found that the 30-year trends at Honolulu varied irregularly from 0.12 cm/year to 0.25 cm/year. At San Francisco the trends were low (about 0.05 cm/year) for the 1904-35 period, rising gradually and leveling off at about 0.25 cm/year for 30-year periods starting after 1915. Since not enough is known about the possible meteorological and oceanographic contributions to these trends, only the long-term linear trends shown in Figure 2 have been eliminated.

ADJUSTMENT FOR ATMOSPHERIC PRESSURE

There is general agreement that for periods of 1 month or more the ocean maintains an isostatic equilibrium with changes in atmospheric pressure. Assuming the average pressure over the whole ocean to be constant, if the pressure difference between two locations changes, the elevation of the sea surface changes in a compensatory manner so that there is no change in distribution of pressure on the sea floor. There is no balancing current associated with this portion of the slope of the sea surface which is balanced by the atmospheric pressure gradient. There-

[2] Formerly the Coast and Geodetic Survey, Environmental Science Services Administration.

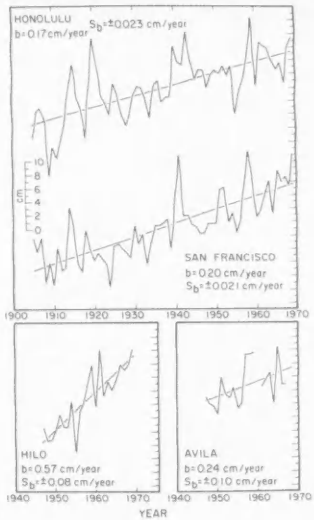

FIGURE 2.—Changes in annual mean sea level at four tide stations and linear trends determined by least squares regression. Slope of regression, b, and standard error of regression, s_b, are shown.

fore, an adjustment for this "inverted barometer" effect is made by correcting the sea levels to a "normal" atmospheric pressure which compensates for both the normal seasonal cycle and the monthly anomaly of atmospheric pressure at the station. For our purpose a correction of 1 cm in sea level for 1 mb change in atmospheric pressure is sufficiently accurate. Adjustments of less than 1 cm for monthly deviations of mean atmospheric pressure over the world oceans reported by Pattullo et al. (1955) have not been made to the individual station data reported here, because they are small and would have no effect on sea level differences.

Monthly mean atmospheric pressure reduced to sea level from weather observations of the National Weather Service at Honolulu, San Francisco, Hilo, and Santa Maria (less than 20 nautical miles from Avila) were obtained mainly from published sources. The World Weather Record series (Clayton, 1944a, 1944b; Clayton and Clayton, 1947; U.S. Weather Bureau, 1959, 1965, 1968) contain climatological data, including monthly atmospheric pressure, through 1960. Monthly mean pressures for first order weather stations are included in the monthly issues of Climatological Data, National Summary, U.S. Environmental Data Service, published since January 1950. Some manuscript records obtained directly from the Weather Service offices were helpful in standardizing all pressure data to sea level.

NORMAL SEASONAL CYCLES OF SEA LEVEL AND SEA LEVEL DIFFERENCE

The *normal* monthly sea levels are obtained by averaging the monthly sea levels[3] for a given month from all years of record. Because the zero level for the scale on the tide gauge is arbitrary at each station the normal monthly sea levels are shown in Table 1 in terms of departure from the long-term mean for all months and years. The standard deviations for given months in Table 1 are measures of the year-to-year variability of monthly sea level for the given month. From these one can compute that the 95% confidence limits on the monthly normals for Honolulu and San Francisco are 0.8 cm or less, and 1.4 cm or less for Hilo and Avila.

We are interested in the real differences in normal monthly sea level between stations as a base against which to measure the variability. For continental stations it is possible to determine this difference of long-term mean sea level between two stations by reference to the geodetic leveling network,[4] but no such reference leveling exists between the continent and Hawaiian Islands. As described in the next section, the long-term sea level difference has been estimated using oceanographic data.

COMPUTATION OF LONG-TERM MEAN SEA LEVEL DIFFERENCE

The long-term mean sea level differences between Honolulu and San Francisco and between

[3] Monthly sea level with trend removed and adjusted to normal atmospheric pressure is hereafter implied.

[4] From oceanographic data, however, Sturges (1966) suggests there may be some systematic north-south leveling error.

TABLE 1.—Departures of normal monthly sea level, $\bar{h}$, from the long-term mean at each tide station; normal monthly sea level difference, $\bar{d}$; and standard deviations, s, of monthly values for total years of record, in centimeters. Honolulu and San Francisco, 1905-69; Hilo and Avila, 1947-59 and 1961-67.

Month	Honolulu		San Francisco		Honolulu-San Francisco		Hilo		Avila		Hilo-Avila	
	$\bar{h}$	s_h	$\bar{h}$	s_h	$\bar{d}$	s_d	$\bar{h}$	s_h	$\bar{h}$	s_h	$\bar{d}$	s_d
Jan.	−1.9	4.4	5.4	5.3	50.6	6.9	−2.0	4.2	4.6	4.4	46.0	4.2
Feb.	−1.7	4.4	4.4	6.3	51.9	6.8	−3.1	3.7	1.1	4.3	47.6	4.4
Mar.	−1.7	5.1	−1.1	6.0	57.4	7.6	−2.9	5.1	−4.6	3.8	53.3	6.3
Apr.	−2.8	5.3	−5.1	4.6	60.3	7.2	−2.2	4.2	−6.9	3.5	56.6	6.0
May	−2.6	5.1	−6.3	3.4	61.7	5.8	−3.5	5.3	−6.6	3.6	55.7	5.6
June	−2.0	5.6	−4.6	2.6	60.6	6.3	−2.5	5.9	−4.3	2.9	53.9	6.0
July	0.3	5.8	−1.3	2.8	59.6	6.4	0.9	5.0	0.0	3.6	53.3	5.2
Aug.	2.6	5.5	−0.5	2.8	61.1	5.8	4.0	4.6	2.2	3.6	53.9	4.7
Sept.	3.7	4.7	1.0	3.2	60.8	5.7	4.4	4.7	3.2	3.7	53.1	6.4
Oct.	3.7	4.7	1.0	3.7	60.7	6.1	4.1	3.5	3.2	4.4	52.9	4.5
Nov.	2.1	3.9	2.3	4.4	57.8	5.8	2.8	4.3	3.8	3.7	50.6	4.8
Dec.	0.1	4.5	4.6	4.9	53.5	6.3	0.0	5.1	4.4	5.1	47.0	5.5

Note: Long-term mean differences, Honolulu-minus-San Francisco and Hilo-minus-Avila, have been adjusted to 58 cm and 52 cm, respectively, by reference to 0/1,000 db dynamic heights, as described in text.

Hilo and Avila have been estimated from 0/1,000 db dynamic height anomalies. Reed (1970) has shown that the real topography of the 1,000 db surface between Honolulu and San Francisco is probably 1 cm or less.

The dynamic height anomalies were obtained from listings of hydrographic station data supplied by the National Oceanographic Data Center and data reports of the Trade Wind Zone Oceanography (TWZO) Program (Charnell, Au, and Seckel, 1967a, b, c, d, e, f).

Information on the number of stations, location, and average dynamic height anomalies is given in Table 2. The locations of the hydrographic stations relative to the tide stations are shown in Figure 3. Frequent observations made since 1949 by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) made it possible to get a good sampling of stations very near the two California tide stations. The density of sampling was much lower near the Hawaiian Islands, so observations over broader geographic regions were used. The mean dynamic height anomalies were computed for several independent sets of observations in the vicinity of Honolulu and Hilo to reveal the extent of island effects, but no large differences were found in the averages.

All oceanographic stations were taken since 1947. Sampling of different months throughout the year was good. Long-term mean Honolulu-minus-San Francisco sea level difference was found to be 58 cm and the Hilo-minus-Avila difference was 52 cm. The normal monthly sea level differences in Table 1 reflect the adjustment of long-term mean sea level differences to these values.

HONOLULU-MINUS-SAN FRANCISCO

The seasonal variation of the normal monthly sea level difference for Honolulu-minus-San Francisco sea level difference is shown in the upper part of Figure 4. The cycle is asymmetric about the mean level. The monthly difference is high, forming a plateau, in the months from April through October, and a sharp minimum occurs from December through February. March and November are transitional months. The range of the normal seasonal cycle is 11 cm or 19% of the long-term mean difference of 58 cm.

The lower part of Figure 4 shows how the normal seasonal cycles at each station contribute to the seasonal cycle of the difference. The monthly normal at San Francisco is lowest in May, early in the upwelling season. The Honolulu sea level is also at its minimum, but the magnitude of the negative departure at San Francisco is more than double that at Honolulu and the normal cycle of sea level difference is at its maximum. Both station curves rise at nearly the same rate from June to October. A somewhat more rapid rise in July at San Francisco,

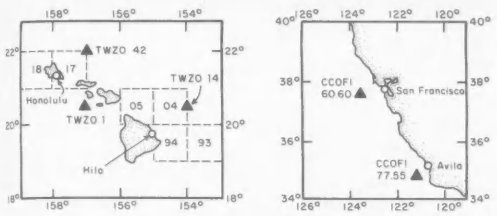

FIGURE 3.—Locations of hydrographic station data used to determine long-term differences in sea level as referred to in text and in Table 2. CCOFI = California Cooperative Oceanic Fisheries Investigations. TWZO = Trade Wind Zone Oceanography program. Two-digit numbers are 1-degree square (dashed lines) identification used in National Oceanographic Data Center listings of hydrographic station data.

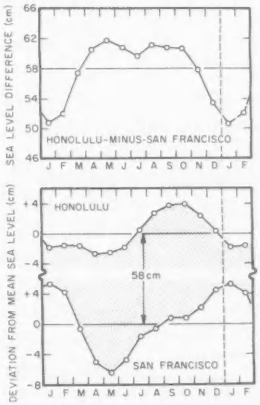
SEA LEVEL DIFFERENCE (cm)
HONOLULU-MINUS-SAN FRANCISCO
J F M A M J J A S O N D J F
DEVIATION FROM MEAN SEA LEVEL (cm)
HONOLULU
58cm
SAN FRANCISCO

FIGURE 4.—Seasonal deviations of 65-year normal (1905-69) monthly sea levels (trend removed and adjusted to normal pressure) from long-term mean, Honolulu and San Francisco (below). Seasonal cycle of normal monthly sea level difference (above). Difference of long-term mean sea level of 58 cm was determined from hydrographic station data (see text).

probably due to heating, giving way to a more gradual rise into autumn, results in a slight dip during July in the plateau of the difference. The sea level at Honolulu drops rapidly from October to January. At San Francisco, however, the sea level continues to rise from November to its highest value in January. Some of this rise is undoubtedly the result of the frequent occurrence of the north-flowing coastal countercurrent in these months (Reid, Roden, and Wyllie, 1958), while some may be due to decrease in the speed of the south-flowing current offshore. The proportions cannot be determined from the sea level data. The combined changes at Honolulu and at San Francisco result in a sharp winter minimum in the normal cycle of sea level difference.

HILO-MINUS-AVILA

The seasonal variation of the normal monthly sea level difference for Hilo-minus-Avila (Figure 5) is similar to that for Honolulu-San Francisco. A winter minimum occurs in December-February, and the maximum occurs in the spring. However, after a decrease of a few centimeters to July the normal difference remains at a nearly constant level through October rather than rising again as it did for Honolulu-San Francisco. March and November are transitional months except that March has a normal difference as high as those for late summer. The range of the normal seasonal cycle

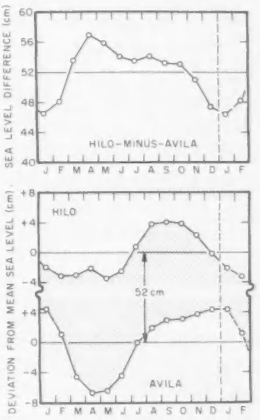

FIGURE 5.—Seasonal deviations of 20-year normal (1947-59, 1961-67) monthly sea level (trend removed and adjusted to normal pressure) from long-term mean, Hilo and Avila (below). Seasonal cycle of normal monthly sea level difference (above). Difference between long-term mean sea level of 52 cm was determined from hydrographic station data (see text).

is 10.6 cm, or 20% of the long-term mean sea level difference of 52 cm.

The seasonal cycle for Hilo is very much like that at Honolulu. The slight peak in April at Hilo, which does not occur at Honolulu, combined with the April minimum at Avila causes the maximum in the sea level difference to occur 1 month earlier for Hilo-Avila than for Honolulu-San Francisco. The normal seasonal cycle at Avila tends to lead that at San Francisco by 1 month. A stronger rise occurs at Avila in June-August than at San Francisco, which may be a heating effect because Avila is at a lower latitude.

DISCUSSION

The characteristics of the normal seasonal cycles of sea level difference for both pairs of stations are in agreement with each other and in accord with our knowledge from other sources of the oceanography of the northeast Pacific and California Current. The geostrophic equation requires that the speed of the surface current be proportional to the transverse slope of the sea surface. From the sea level difference we can infer that the average current normal to the great circles between the Hawaiian Islands and the California coast is southeastward throughout the year. It is strongest in the upwelling and summer season when the North Pacific atmospheric high pressure cell is best developed. It is weakest during the winter season.

Using an average latitude between stations and the long-term differences in the geostrophic equation, the average current to the southeast is 2.0 cm/sec for the Honolulu-San Francisco difference and 1.9 cm/sec for the Hilo-Avila difference. The range of the normal seasonal cycle, as noted earlier, is 20%.

It must be kept in mind that the sea level difference indicates only the average geostrophic surface current normal to the line between the two stations. For the California Current the contours of 0/500 db dynamic height anomaly in the CalCOFI Atlas No. 4, Geostrophic Flow (Wyllie, 1966) indicate that the speed averaged over a distance of 1,000 km is about 5 to 10 cm/sec, whereas there may be narrow regions about 100 km in width with current of 25 cm/sec, or greater.

COMPARISON OF MONTHLY SEA LEVELS WITH STERIC LEVELS

Monthly sea level differences are to be used to estimate the slope of the sea surface and draw inferences regarding month-to-month and year-to-year changes in current from the geostrophic equation. Traditionally the slope is estimated indirectly by computing geopotential heights, or steric levels. Therefore, the agreement between monthly sea levels and steric levels at nearby offshore locations was investigated using hydrographic station data, employed earlier to establish the long-term mean differences in sea level between pairs of stations. Correlation coefficients between the monthly sea levels, linearly interpolated to the date of each hydrographic station, and the steric levels are given in the last column of Table 2. For San Francisco and Avila, where a large number of hydrographic stations were made within a small area at nearby locations, the correlation coefficients are 0.54 and 0.57 respectively. Both coefficients are considerably higher than the 1% level of significance.

For Honolulu the correlations from four sets of data from different areas are quite consistent, ranging from 0.54 to 0.65. These coefficients are as large as those for San Francisco and Avila, but because of the smaller sample sizes are statistically significant only at the 5% level.

For Hilo the correlations for three different sets of steric levels are less consistent. A high correlation, $r = 0.78$, which is significant at the 1% level, was obtained with Hilo monthly sea levels only from the set of 10 steric levels from observations in 1-degree squares 04 and 05 immediately northeast of Hilo. Dynamic topography charts in TWZO data reports (Charnell et al., 1967a, b, c, d, e, f) reveal that the presence of an anticyclonic eddy or ridge northeast of Hilo at TWZO station 14 during 5 of the 16 observational periods caused the lower correlation of data from that station with Hilo sea levels. One suspects some similar local effect as

TABLE 2.—Determinations of long-term mean sea level differences from 0/1,000 db geopotential (steric) anomalies at nearby offshore locations. Correlations, r, of monthly sea levels with geopotential anomalies.

Shore station	Data source	Location of hydrographic stations (see Figure 3)	Distance from shore station (km)	No. of observations	Average steric anomaly, 0/1,000 db (dyn cm)	Correlation, r steric vs. sea level
Honolulu	NODC	1-degree square 17, Marsden square 088	10-100	10	[1] 182.4	0.65*
	NODC	1-degree square 18, Marsden square 088	30-120	12	[1] 182.2	0.64*
	TWZO	Station 1	100	16	184.3	0.60*
	TWZO	Station 42	120	15	184.0	0.54*
San Francisco	NODC	CalCOFI 60.60	105	52	[2] 125.2	0.54**
		Long-term mean sea level difference, Honolulu-minus-San Francisco = 58 cm				
Hilo	NODC	1-degree squares 04, 05, Marsden square 088	10-150	11	[1] 179.5	0.78**
	NODC	1-degree squares 93, 94; Marsden square 052	20-200	10	[1] 179.3	0.48
	TWZO	Station 14	140	16	181.1	0.42
Avila	NODC	CalCOFI 77.55	50	42	[3] 127.5	0.57**
		Long-term mean sea level difference, Hilo-minus-Avila = 52 cm				

[1] 0/500 db average plus 49.0 dyn cm for 500/1,000 db average, based on TWZO data and 1,000 m stations.
[2] 0/500 db average plus 45.9 dyn cm for 500/1,000 db average, based on 37 stations in same 1-degree square.
[3] 0/400 db average plus 57.9 dyn cm for 400/1,000 db average, based on 25 stations in same 1-degree square.
* Correlation significant at 5% level.
** Correlation significant at 1% level.

the cause of the lower correlation for observations in 1-degree squares 93 and 95.

The correlations between monthly sea levels and offshore steric levels for the four stations in this study are less than anticipated from the results reported by other investigators, e.g., Shaw and Donn (1964) and Sturges (1966), as noted in the section, Earlier Studies. It is suspected that the lower correlations for the four Pacific stations in the present study may be due in part to comparison of a monthly sea level with a steric level from a single hydrographic observation on a given day. Present available steric data explain only about 40% of the variance of monthly sea levels from which the trend has been removed and which have been adjusted to normal pressure. As suggested by Stommel (1958) in relation to sea level at Bermuda, the possibility exists that geostrophically balanced barotropic currents exist which would also affect the monthly mean sea levels. When time series of frequent hydrographic observations or long-term observations from buoys become available to give a better estimate of continuous changes in steric level, we may then be able to attain a better understanding of the causes of sea level variations. For the present the unexplained variability may limit the use of sea levels and sea level differences to interpretation of broad-scale, highly anomalous oceanic changes.

NONSEASONAL SEA LEVEL DIFFERENCES

The monthly sea level differences used in this study are given in Appendix Tables 1 and 2 for Honolulu-minus-San Francisco and Hilo-minus-Avila, respectively. For each station the linear trends were removed and values adjusted to normal atmospheric pressure. The monthly differences reflect the adjustment, previously discussed, of the long-term mean sea level difference for all months and years to a mean difference determined from 0/1,000 db geopotential heights.

VARIABILITY

The nonseasonal variations are represented by the monthly anomalies, defined as the difference between the value for the month and the normal for the same month. The standard deviations in Table 1 for given months at individual stations exhibit the same characteristics as those reported in an earlier study (Saur, 1962) for six Pacific

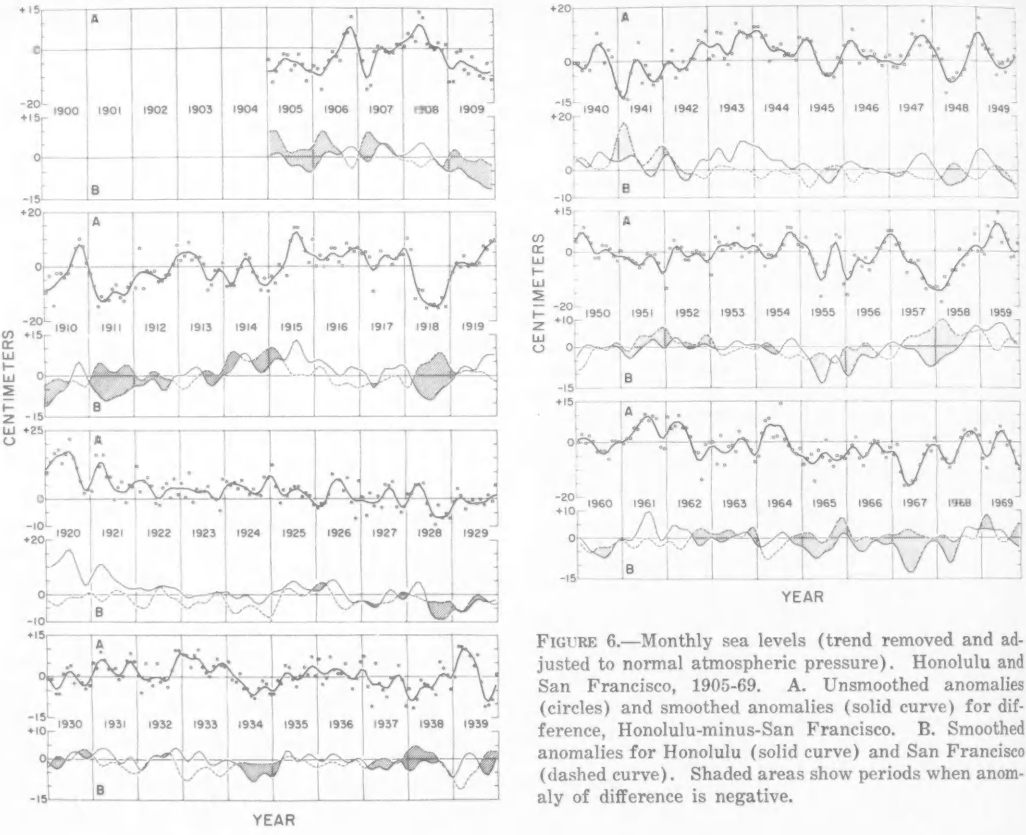

FIGURE 6.—Monthly sea levels (trend removed and adjusted to normal atmospheric pressure). Honolulu and San Francisco, 1905-69. A. Unsmoothed anomalies (circles) and smoothed anomalies (solid curve) for difference, Honolulu-minus-San Francisco. B. Smoothed anomalies for Honolulu (solid curve) and San Francisco (dashed curve). Shaded areas show periods when anomaly of difference is negative.

stations, two of which were Honolulu and San Francisco. Standard deviations in the former study were slightly larger because trends were not eliminated. At San Francisco, a coastal station at mid-latitude, the standard deviations show a seasonal change, attaining values near 6 cm in the late winter but decreasing to less than 3 cm in summer. At the other stations they vary less with season and those at the island stations generally lie in the range between 4.0 and 5.5 cm.

The standard deviations of the monthly sea level differences (Table 1) do not vary greatly throughout the year. The Honolulu-minus-San Francisco values are slightly larger than those for Hilo-minus-Avila because "climatic" changes, to be discussed later, appear in the longer Honolulu-San Francisco records.

The time series of the anomalies of monthly sea level difference are shown by open circles in Figure 6 for Honolulu-minus-San Francisco and in Figure 7 for Hilo-minus-Avila. The variability indicated by the standard deviations is evident. To suppress the shorter period variability and aid in detecting underlying longer period changes the time series have been smoothed, as indicated by the solid curves.

A simple 5-point smoothing operator with weights of $-1/16$, $1/4$, $5/8$, $1/4$, $-1/16$ was selected for the smoothing. This is a particular case of one-dimensional, two-element smoothers described by Shapiro (1970). It is a low-pass filter with a response function:

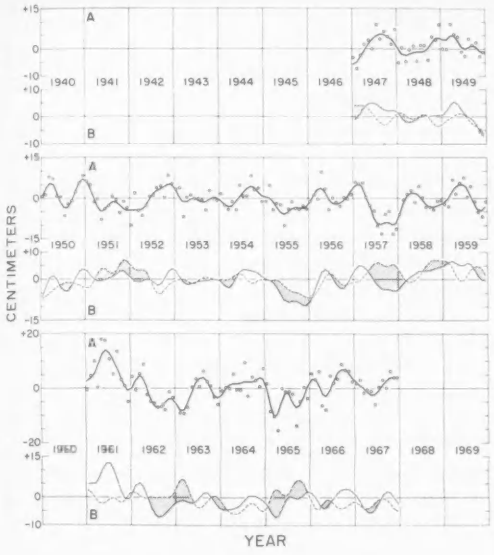

FIGURE 7.—Monthly sea levels (trend removed and adjusted to normal atmospheric pressure). Hilo and Avila, 1947-59 and 1961-67. A. Unsmoothed anomalies (circles) and smoothed anomalies (solid curve) for difference, Hilo-minus-Avila. B. Smoothed anomalies for Hilo (solid curve) and Avila (dashed curve). Shaded areas show periods when anomaly of difference is negative.

$$R(n) = 1 - \sin^4 \frac{\pi}{n}$$

where n is the number of data intervals in the Fourier component being smoothed. In our case n is also the wave period in months. Periods of 2 months are eliminated completely in one application of the smoother. Repeated applications of the smoother eliminate or reduce progressively longer periods. The response is a positive value between zero and one for all finite wave periods, so no 180° phase shift nor amplification occurs. The filter can be applied to the individual station anomalies followed by computation of the difference, or applied directly to the time series of the difference anomalies with the same end result.

The smoothed anomalies of monthly sea level for each station and of sea level differences in Figures 6 and 7 were obtained by applying the smoother eight successive times. The 50% level for the response function lies between periods of 5 and 6 months, and the response is 85% at 8 months.

CORRELATIONS BETWEEN HONOLULU-MINUS-SAN FRANCISCO AND HILO-MINUS-AVILA ANOMALIES

There are no independent data against which to check the anomalies of sea level differences as an index of nonseasonal variations in current. Since the two sets of differences span very nearly the same current region, the consistency between them is examined in this section to see if they agree reasonably well.

The correlations by month for both unsmoothed and smoothed anomalies are listed in Table 3. A general improvement of the correlations, particularly in winter, occurs as a result of smoothing to suppress the short-period variability. The effect of different scales of wind systems can be recognized by the seasonal pattern of correlations, especially in the smoothed anomalies. In the months from April through November when the subtropical high dominates the atmospheric pressure pattern over the North Pacific Ocean, all the correlations of smoothed anomalies are significant at the 1% level. In the months from November through March when meso-scale cyclonic and anticyclonic

TABLE 3.—Correlations of monthly sea level differences, by month Hilo-minus-Avila versus Honolulu-minus-San Francisco; $n = 20$ years.

Month	Unsmoothed anomalies	Smoothed anomalies
January	0.37	0.45*
February	0.37	0.44*
March	0.40	0.48*
April	0.56**	0.54**
May	0.45*	0.58**
June	0.63**	0.63**
July	0.64**	0.63**
August	0.41	0.69**
September	0.74**	0.68**
October	0.53**	0.56**
November	0.32	0.51*
December	0.57**	0.49*

* Correlation significant at 5% level ($r \geq 0.42$).
** Correlation significant at 1% level ($r \geq 0.54$).

wind systems move through the region, the correlations are somewhat lower, but still significant at the 5% level.

For the entire 20 years of concurrent records for Hilo-minus-Avila and Honolulu-minus-San Francisco, the correlation of unsmoothed anomalies is 0.49 and for smoothed anomalies it is 0.55. The 1% level of significance for the correlation coefficient of a sample of 240 months is 0.17, so these values are highly significant.

A visual comparison of the data in Figures 6 and 7 reveals the agreement evidenced by the correlation coefficients. Smoothed anomalies of the same sign tend to occur at the same time. For the most part the oscillations of the smoothed anomalies of sea level difference are in phase. Oscillations are noticeably out of phase in the periods October 1950-February 1951, March 1952-January 1953, September 1955-June 1956, and January-July 1958. In the last 18 months of the Hilo-minus-Avila record (July 1966-December 1967) the changes are similar to those for Honolulu-minus-San Francisco, but the smoothed anomaly of the difference is positive rather than strongly negative. Except for the 1955 periods, the nonagreement of the anomalies during these periods results mainly from a rise in sea level at San Francisco as opposed to a drop at Avila. These periods comprise only 20% of the total 20-year coincident records. In the remaining 80% the correlation coefficient for unsmoothed anomalies is 0.65 and for the smoothed anomalies it is 0.76. Both are significant well beyond the 1% level of 0.186 for a sample of 190.

CURRENT CHANGES INFERRED FROM SEA LEVEL DIFFERENCES

In this section some characteristics of the 65-year record of anomalies of sea level differences, Honolulu-minus-San Francisco are described with emphasis on their implications regarding changes in surface currents. Because the smoothed anomalies minimize local effects near the station, such as the set-up by wind and eddy systems passing near the Hawaiian Islands, they will be used as more realistic estimates of the larger scale and longer term changes in circulation. The term *current index* will be applied to this usage.

The discussion will follow the basic premise in this paper, that the currents are geostrophically related to the sea level difference so that a positive current index indicates above normal current, i.e., stronger flow to the south around the eastern limb of the anticyclonic gyre of the North Pacific Ocean. Conversely, negative current indexes indicate a below-average slope of the sea surface and proportionally weaker circulation.

Three tables have been compiled to show the characteristics of the current indexes. Table 4 gives statistical data regarding the current indexes by month. The data describe the year-to-year variations that occur. The normal monthly sea level differences, d, (of unsmoothed data) are repeated from Table 1 as a reference against which to measure the ranges and standard deviations of the current indexes.

Visual inspection of the time series (Figure 6) indicates that there are a number of different "climatic periods" in the record, i.e., periods characterized by the variability and the mean level of the current index during the period. Table 5 identifies seven such periods, into which I have subjectively divided the time series, and gives the mean and the standard deviation about that mean for each period. Obviously, other investigators might well select different climatic periods based upon other criteria related to their work.

In Table 6, highly anomalous periods have been identified on the basis of a criterion that the magnitude of the current index exceeded 10 cm for two or more consecutive months. As well as information on the dates, sign, magnitude, and duration of the current index, data are also given on the sign, magnitude, and date of the largest monthly sea level index at Honolulu and San Francisco which coincided with the current index greater than 10 cm.

Some observations which may be made about the Honolulu-minus-San Francisco differences and the information in these tables are given below.

1. The standard deviations of year-to-year changes for a given month (Table 4) vary from

TABLE 4.—Variability of current index (smoothed anomaly of sea level difference), Honolulu-minus-San Francisco, by months. $N = 65$ years. Standard deviation (s); largest positive and negative departures (Max and Min) and year of occurrence; Range (R) in centimeters and in percent of normal monthly sea level difference, $\bar{d}$ (from Table 1).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
s (cm)	5.7	6.0	6.2	6.0	5.7	5.5	5.4	5.2	5.1	5.2	5.3	5.4
Max (cm)	11.2	13.5	15.3	16.0	16.5	17.4	17.7	15.8	11.4	10.3	9.5	10.6
Year	1920	1920	1920	1920	1920	1920	1920	1920	1920	1943	1943	1948
Min (cm)	−14.7	−14.4	−13.0	−14.0	−16.1	−15.4	−14.2	−14.6	−14.5	−13.5	−13.7	−14.4
Year	1958	1958	1958	1967	1967	1967	1918	1918	1918	1918	1957	1957
R (cm)	25.9	27.9	28.4	30.1	32.6	32.7	31.9	30.4	25.9	23.8	23.2	25.0
$R/\bar{d}$, (%)	52	54	49	50	53	54	53	49	43	39	40	47
$\bar{d}$ (cm)	50.6	51.9	57.4	60.3	61.7	60.6	59.6	61.1	60.8	60.7	57.8	53.5

5.1 cm in September to 6.2 cm in March. The seasonal change is due to greater winter-time variability at San Francisco (Saur, 1962) probably caused by year-to-year differences in weather conditions. A range of two standard deviations is nearly the same as the 11 cm range of the normal seasonal cycle. Long-term non-seasonal changes exceed ± 10% of the normal over one-third of the time.

2. The range between extremes (Table 4) in any given month varies from 23.2 cm for November to 33.7 cm in June. These are 39% and 54%, respectively, of the normal sea level differences for these months.

3. The minimum current index was —16.1 cm in May 1967 and the maximum was +17.7 cm in July 1920. The range between the extremes of the current index is 58% of the long-term mean sea level difference of 58 cm for Honolulu-minus-San Francisco, and it is three times as large as the range of the normal seasonal cycle.

4. The periods 1905-15, 1939-41, and 1955-69 were characterized by large changes between positive and negative values of current index over periods up to a few years, but on the average the indicated current is weaker than normal (Table 5).

5. During the periods 1915-25 and 1942-49, the current index implies moderate to large changes in current over periods of several years but indicates on the average a current stronger than normal. Except for large negative values in 1918, the current index indicates almost continuously stronger-than-normal circulation from mid-1915 through 1925.

6. The current changes during the periods 1926-38 and 1950-54 were relatively small as compared to the rest of the records. The current index did not exceed 8.5 cm and was nearly evenly distributed between negative and positive values.

7. The sea level records imply that unusually weak currents (negative anomalies in Table 6) occurred in 1911, 1918, 1941, 1957-58, and 1967, and that the periods of unusually strong currents occurred in 1915, 1920-21, 1943-44, 1948-49, and 1959.

8. During 7 of the 10 highly anomalous periods in Table 6, the absolute value of the monthly sea level anomaly at Honolulu is much larger than that at San Francisco. This indicates that significant changes in physical conditions which affect circulation occur in the central water of the current gyre as well as in the boundary current itself.

CONCLUDING REMARKS

For the investigation of historical changes in the ocean environment two notable observational deficiencies are apparent: the paucity of time-series subsurface data and the lack of information on changes in current of periods from a few months to several years. This study has attempted to develop some information on the normal seasonal cycle and the nonseasonal change of ocean currents in that part of the eastern

TABLE 5.—Mean current index, $\bar{\Delta}d$, and standard deviation, s, Honolulu-minus-San Francisco, for selected "climatic" periods (see text).

Years	Number of months	$\bar{\Delta}d$ (cm)	s (cm)
1905-14	120	−3.0	5.3
1915-25	132	3.5	6.1
1926-38	156	0.2	3.6
1939-41	36	−1.2	6.3
1942-49	96	2.6	4.8
1950-54	60	0.1	3.4
1955-69	180	−1.9	5.6

North Pacific Ocean which includes the California Current, using the most appropriate long-term records of sea level available.

Monthly sea level differences for a 65-year period (1905-69) between Honolulu and San Francisco and for 20 years (1947-59, 1961-67) between Hilo and Avila were computed to indicate the strength and fluctuations in the monthly geostrophic current around the eastern limb of the anticyclonic gyre of the North Pacific Ocean. The premise is that through the geostrophic relationship the nonseasonal variations of sea level difference indicate proportional changes in the current.

The distance between tide stations in each pair is about 3,900 km. The current structure is not uniform across the geographic region. Variability in the records is introduced by local conditions, and smoothing has been used to minimize these effects. Therefore, the sea level differences presented here can be indicative of only large-scale changes in circulation and conclusions regarding the circulation have been confined to periods of the more persistent highly anomalous periods in the sea level differences. In the tropical and western North Pacific where islands are more suitably located with respect to the currents the procedures followed here might be used to study variations in the Equatorial Currents and the Kuroshio.

In the Northeast Pacific there is no independent set of long-term observations to substantiate the inferences regarding current changes that have been drawn and no other islands for improving the network of tide stations. This lack emphasizes the desirability of frequent sections of subsurface observations between Cali-

TABLE 6.—Highly anomalous periods of sea level difference Honolulu-minus-San Francisco, 1905-69, identified by current index magnitude greater than 10 cm for at least two consecutive months.

Difference[1]												
1. Sign of anomaly	Negative	Positive	Negative	Positive	Negative	Positive	Positive	Positive	Negative	Positive	Negative	
2. No. of months, magnitude of anomaly >10 cm	4, (1)[3]	3	7	9, (3)	3	2, (2)	2	6	2	4		
3. Dates, magnitude of anomaly >10 cm	Mar.-June 1911 (Oct. 1911)	July-Sept. 1915	May-Nov. 1918	Jan.-Sept. 1920 {Feb.-Apr. 1921}	Jan.-Mar. 1941	Sept.-Oct. 1943 (Jan.-Feb. 1944)	Dec. 1948-Jan. 1949	Oct. 1957-Apr. 1958	May-June 1959	Apr. 1967-July 1967		
4. Largest anomaly, cm	−12.8	+12.9	−14.6	+17.7, (+13.7)	−13.6	+11.2 (+11.2)	+10.9	−14.7	+10.3	−16.1		
5. Total months duration, anomaly of same sign	22	23	11	80	23	32	8	18	19	45		
6. Inclusive dates for 5	Jan. 1911-Oct. 1912	May 1915-Mar. 1917	Mar. 1918-Jan. 1919	Feb. 1919-Oct. 1925[3]	Oct. 1940-Aug. 1942[4]	Sept. 1942-May 1945	Oct. 1948-May 1949	Apr. 1957-Sept. 1958	Oct. 1958-Apr. 1960[5]	Sept. 1964-June 1968		
Honolulu[1]												
7. Sign of anomaly	Negative	Positive	Negative	Positive	Positive	Positive	Positive	Negative	Positive	Negative		
8. Largest anomaly, cm, during 3 above	−9.4	+13.1	−9.2	+16.6 (+11.0)	+5.0	+10.6 (+8.5)	+7.8	−7.6	+9.2	−12.4		
9. Date of largest anomaly	May 1911	Aug. 1915	July 1918	July 1920, Mar. 1921	Mar. 1941	Sept. 1943, Jan. 1944	Jan. 1949	Nov. 1957	June 1959	May 1967		
San Francisco[1]												
10. Sign of anomaly	Positive	Positive	Positive	Negative	Positive	Negative	Negative	Positive	Negative	Positive		
11. Largest anomaly, cm, during 3 above	+4.6	+0.4	8.6	−4.2, (−2.7)	+17.7	0, −3.3	−3.8	+10.0	−1.6	+3.7		
12. Date of largest anomaly	Mar. 1911	Sept. 1915	Oct. 1918	Mar. 1920, Mar. 1921	Feb. 1941	Sept. 1943, Feb. 1944	Dec. 1948	Feb. 1958	May 1959	May 1967		

[1] All data refer to the smoothed anomalies depicted in Figure 6.
[2] ( ) secondary maximum or minimum in the same period.
[3] Ignores −0.4 cm in October 1923.
[4] Ignores +0.9 in June 1941.
[5] Ignores −0.3 cm in November 1959.

fornia and Hawaii. One would like information on the strength of the California Current, on the role of upwelling in the variations of the current, about the movement of the boundary or transition zone between the central water mass and the waters of the California Current, and about the interconnection between the California Current and the North Equatorial Current. The large changes in sea level at Honolulu as compared to San Francisco during periods of strong anomalies in the sea level difference (Table 6) raise the question as to how the California Current may vary in strength or width in relation to changes in the central water mass and position of the eastern North Pacific anticyclonic current gyre. Such environmental information has important applications for advisory services and forecasting for fisheries along the west coast of the United States.

One consequence of the preliminary work with sea level differences (Saur, 1966) mentioned earlier was the start of a pilot program of expendable bathythermograph observations between Honolulu and San Francisco aboard a merchant ship (Saur and Stewart, 1967) in June 1966, which continued at a frequency of up to 20 sections per year through 1970. Although the period of observation is very short as compared to the sea level records, it is hoped that the analysis of these observations can better define conditions related to the anomalous weak circulation in 1967 inferred from the sea level records, and shed light on the more specific problems mentioned above.

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APPENDIX TABLE 1.—Honolulu-minus-San Francisco, 1905-69. Monthly sea level difference (linear trend removed and adjusted to normal atmospheric pressure at each station) in centimeters. The long-term mean difference for all months and years has been adjusted to 58 cm, as explained in text, by reference to 0/1,000 db geopotential heights.

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1905	46.7	39.5	48.6	54.7	59.6	58.2	51.5	54.8	58.6	54.9	45.9	45.2
1906	43.8	44.1	42.1	52.9	(57.3)[1]	59.2	56.6	56.3	65.9	66.6	69.4	58.1
1907	50.2	47.1	42.3	46.8	60.5	61.5	59.6	59.6	58.9	59.0	59.4	55.1
1908	51.5	57.6	61.5	62.8	75.1	72.0	61.1	61.5	60.2	62.8	56.9	54.8
1909	38.4	39.9	56.0	59.6	53.7	51.3	56.6	54.2	50.7	49.7	52.4	41.9
1910	41.8	48.8	43.0	58.0	59.4	56.6	57.3	61.8	67.2	71.4	65.4	54.7
1911	48.0	44.7	42.6	49.7	49.2	48.5	51.7	54.7	49.3	48.0	50.4	47.6
1912	42.8	58.9	49.3	59.0	59.4	59.1	54.0	55.9	57.7	57.9	58.9	61.6
1913	52.8	55.9	66.5	62.7	65.4	64.1	60.6	52.4	54.0	59.4	56.8	55.0
1914	43.3	45.0	50.5	59.3	61.6	65.3	62.7	58.9	56.9	51.9	53.7	44.4
1915	47.2	45.7	58.2	59.9	58.2	69.2	74.2	75.5	70.4	66.5	59.2	63.6
1916	50.7	56.2	57.1	63.0	68.6	67.5	61.2	61.0	69.4	67.3	63.2	60.7
1917	55.3	57.5	60.7	51.2	62.0	66.5	64.3	64.8	61.3	63.7	62.3	57.7
1918	61.3	58.2	45.5	51.9	52.7	45.3	45.8	47.2	45.3	49.4	43.0	48.0
1919	48.5	53.2	56.9	64.3	61.4	61.6	59.8	62.2	68.4	66.8	67.3	62.8
1920	60.4	65.5	73.9	78.4	74.5	76.6	81.6	76.1	72.1	67.5	59.8	56.9
1921	53.4	68.0	68.7	76.6	69.6	68.6	59.1	65.2	67.0	59.1	62.9	57.6
1922	62.6	54.4	63.8	68.3	66.3	58.7	57.1	65.0	66.4	60.8	65.1	54.7
1923	56.3	52.3	66.9	58.8	65.1	63.2	62.2	65.6	61.0	60.8	53.3	60.5
1924	56.7	56.6	63.2	63.7	68.4	64.3	60.9	64.6	62.1	61.6	65.8	60.8
1925	63.0	56.3	55.5	63.7	62.5	64.1	64.0	65.3	61.3	62.8	58.7	51.1
1926	46.9	50.0	55.7	61.9	70.6	67.7	66.3	63.7	68.3	59.1	50.4	59.8
1927	51.0	45.4	59.3	57.3	62.5	57.1	64.7	65.5	66.9	57.5	52.6	50.5
1928	52.2	53.7	62.3	65.6	67.4	58.8	53.2	51.4	58.1	53.4	52.2	46.1
1929	49.3	55.6	58.2	56.2	60.2	59.9	57.4	60.7	58.1	62.0	56.5	58.4
1930	49.5	51.1	50.7	53.8	62.7	63.9	63.7	58.4	61.3	58.3	53.1	50.2
1931	55.7	54.8	66.2	66.5	64.3	63.0	62.8	59.8	61.0	66.5	66.4	58.9
1932	50.9	45.9	62.3	58.9	58.3	65.5	57.6	60.8	56.8	63.1	67.4	62.7
1933	58.5	59.6	60.7	68.1	71.6	64.1	61.2	61.0	64.6	67.4	62.0	57.0
1934	56.1	50.8	55.3	61.7	57.2	56.4	52.6	53.0	56.7	59.4	55.2	47.3
1935	44.2	50.8	54.7	64.6	65.0	60.1	56.0	61.6	64.4	61.4	65.3	53.7
1936	57.2	49.0	57.0	67.7	64.2	61.8	61.0	66.0	60.3	56.2	57.3	59.0
1937	58.3	48.3	46.3	65.4	59.2	55.6	52.0	60.9	60.4	65.0	56.6	42.6
1938	46.5	40.3	49.1	59.4	58.9	57.4	55.1	54.2	66.3	63.6	58.4	48.8
1939	50.7	63.1	68.0	70.3	69.2	64.5	67.7	59.1	49.7	50.5	49.5	54.6
1940	50.0	51.3	53.9	58.9	58.4	65.0	70.3	67.8	60.0	65.1	59.6	43.6
1941	39.1	38.2	43.1	56.0	62.1	67.6	51.5	59.5	55.6	51.8	50.6	47.3
1942	49.0	51.2	61.2	54.0	58.1	60.2	56.3	61.6	61.2	68.2	64.3	64.4
1943	51.1	53.7	67.7	70.2	62.3	58.9	62.2	74.7	71.4	70.4	66.1	62.3
1944	63.0	64.3	65.6	69.5	61.2	65.4	63.6	67.0	62.3	63.2	59.1	53.2
1945	59.0	59.2	65.3	67.1	64.4	58.5	54.7	55.8	55.6	54.2	58.7	52.4
1946	55.6	58.5	68.7	65.4	60.3	64.1	60.3	64.3	62.6	60.0	55.5	54.5
1947	52.5	49.2	54.4	61.9	59.8	62.5	69.3	69.3	65.9	75.3	64.4	57.9
1948	51.9	56.2	57.5	48.3	54.4	54.2	55.1	55.6	57.4	65.9	64.1	63.0
1949	66.7	57.7	61.6	64.4	63.8	55.5	58.8	60.3	56.5	61.6	57.5	55.7
1950	54.5	58.9	66.5	65.9	65.0	58.3	57.3	63.6	63.0	61.8	56.0	49.9
1951	51.3	49.4	54.8	57.0	57.3	54.5	55.0	60.2	59.1	59.7	53.7	45.2
1952	37.0	53.3	61.5	61.3	63.4	57.4	56.3	60.7	61.0	59.6	56.5	49.5
1953	41.8	57.3	60.6	60.7	64.2	61.7	62.0	69.8	58.6	61.8	57.4	59.5
1954	50.6	54.4	51.6	59.1	59.9	58.7	60.4	63.5	69.7	69.4	63.0	55.7
1955	52.1	57.2	56.5	57.1	56.6	44.0	51.6	55.8	62.2	66.9	62.9	41.3
1956	34.5	43.9	55.9	57.7	55.8	58.2	52.5	57.1	62.0	61.7	61.2	61.0
1957	58.2	54.1	60.2	59.5	53.6	57.1	54.9	57.5	50.3	46.6	44.8	39.7
1958	37.6	33.3	47.9	47.8	54.6	53.5	60.5	55.7	59.6	61.2	64.2	53.4
1959	50.8	50.7	66.7	65.4	72.5	75.2	62.9	68.1	65.0	58.6	56.2	56.7
1960	50.3	55.2	57.0	62.9	62.0	56.9	55.8	58.0	54.4	61.3	58.3	53.5
1961	49.9	53.3	58.8	65.6	66.2	68.4	69.9	68.7	70.3	69.3	55.8	50.8
1962	59.9	56.7	63.2	70.2	66.6	65.8	61.4	57.2	56.7	46.9	56.9	53.5
1963	50.8	43.7	59.7	51.8	59.9	59.4	55.9	65.1	61.8	61.0	54.7	46.2
1964	45.5	55.1	65.1	69.0	63.2	62.7	73.8	61.9	59.2	(57.6)[1]	53.2	51.1
1965	42.3	45.9	52.9	45.9	58.6	54.7	60.2	54.0	51.5	55.7	52.2	47.0
1966	46.4	50.6	59.0	54.0	52.8	56.3	59.1	61.5	60.6	56.6	51.8	51.3
1967	45.5	51.0	46.1	44.2	45.6	46.2	45.8	52.5	56.0	59.3	54.1	54.9
1968	48.7	45.4	50.9	50.7	53.9	56.8	61.1	65.3	62.6	63.7	62.3	55.6
1969	44.3	42.1	57.3	58.0	64.8	66.4	63.3	59.5	60.9	57.2	49.8	43.5
N	65	65	65	65	64	65	65	65	65	64	65	65
MEAN	50.6	51.9	57.4	60.3	61.7	60.6	59.6	61.1	60.8	60.7	57.8	53.5

[1]Missing value was estimated by interpolation of anomalies.

APPENDIX TABLE 2.—Hilo-minus-Avila, 1947-59 and 1961-67. Monthly sea level difference (linear trend removed and adjusted to normal atmospheric pressure at each station) in centimeters. The long-term mean difference for all months and years has been adjusted to 52 cm, as explained in text, by reference to 0/1,000 db geopotential heights.

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1947	42.4	40.0	50.9	58.1	58.8	53.7	62.2	57.3	59.5	57.1	52.0	54.1
1948	40.8	47.9	48.5	56.0	56.7	49.2	54.4	54.9	48.7	57.2	53.6	55.9
1949	45.9	47.1	62.5	61.8	59.9	52.8	50.4	57.6	54.2	55.2	47.7	45.7
1950	46.5	48.6	60.9	63.2	55.8	54.1	46.3	51.6	51.7	54.8	56.1	55.1
1951	52.0	52.1	51.5	56.1	47.4	49.8	50.3	54.5	52.0	47.0	49.1	43.1
1952	35.7	49.2	48.3	49.7	52.6	54.3	54.2	57.5	57.4	52.7	58.8	52.1
1953	49.0	51.2	46.3	56.8	56.6	53.5	52.8	52.8	48.3	55.5	50.1	45.7
1954	47.5	44.7	48.7	55.1	51.0	58.6	53.8	54.4	61.2	55.7	54.2	45.4
1955	44.8	52.3	48.7	54.4	52.9	43.6	48.7	52.6	49.0	48.4	47.7	42.6
1956	45.0	48.8	52.7	66.2	58.9	49.4	53.4	52.3	49.8	53.1	50.0	48.3
1957	52.0	52.7	59.1	56.5	52.6	49.2	42.9	40.7	47.2	48.0	37.2	35.7
1958	40.7	47.0	54.9	59.5	53.9	58.4	53.2	50.4	49.7	48.4	49.5	46.1
1959	43.6	44.3	60.2	58.0	61.3	61.5	53.5	58.3	52.0	47.5	43.6	45.7
1960	--	--	--	--	--	--	--	--	--	--	--	--
1961	45.5	52.1	63.3	56.6	73.6	71.3	63.9	59.0	66.6	56.0	51.4	41.8
1962	50.4	46.6	58.7	65.4	53.0	48.9	47.4	46.6	46.3	44.8	49.2	43.3
1963	(39.5)[1]	38.3	43.8	49.4	55.9	57.5	53.8	60.3	55.5	53.6	47.0	40.7
1964	45.0	47.8	53.1	61.9	54.9	53.1	62.8	51.0	57.3	55.8	51.1	54.3
1965	47.9	38.8	42.8	40.9	55.7	52.6	52.0	51.7	39.1	48.0	51.1	43.1
1966	51.6	50.7	59.8	50.1	47.5	58.6	55.1	57.4	62.0	59.5	56.9	49.4
1967	47.8	50.8	51.5	56.1	54.4	47.9	53.9	57.1	53.0	59.3	54.5	51.2
N	19	20	20	20	20	20	20	20	20	20	20	20
MEAN	46.0	47.6	53.3	56.6	55.7	53.9	53.3	53.9	53.0	52.9	50.5	47.0

[1]Missing value was estimated by interpolation of anomalies.

TEMPERATURE TRENDS AND THE DISTRIBUTION OF GROUNDFISH IN CONTINENTAL SHELF WATERS, NOVA SCOTIA TO LONG ISLAND

JOHN B. COLTON, JR.[1]

ABSTRACT

The 1953 to 1967 downward trend in seawater temperature in continental shelf waters between Nova Scotia and Long Island did not significantly alter the distribution of four species of groundfish. There was an extension of the southern range of American plaice and a contraction of the northern range of butterfish. These shifts in distribution were not extensive. The equatorward boundary of American plaice appears to be limited by summer temperatures too high for survival and the poleward boundary of butterfish by summer temperatures too low for reproduction. There was no obvious alteration in the geographic distribution of haddock and yellowtail flounder. The distribution and movements of haddock and yellowtail flounder appear to be influenced more by restrictive spawning area and bottom type conditions than by temperature.

An alternation in sea-surface temperature has been observed at Atlantic coast stations from Nova Scotia to Cape Hatteras (Lauzier, 1965; Stearns, 1965; Welch, 1967). Coastal warming and cooling trends have been pronounced in the waters between Cape Sable and Long Island. A warming trend began in the early 1940's and reached a maximum during 1952-53. This rise in temperature was followed by a cooling period which continued with only minor checks through 1967. Since 1967 there has been an increase in sea-surface temperature, the 1969 annual mean being only slightly lower than the long-term mean. An example of these temperature trends is shown in Figure 1 in which the annual deviations from the 1940-1959 mean sea-surface temperature at Boothbay Harbor, Maine are plotted for the period 1940-1968. The base period 1940-1959 was chosen for it included approximately equal numbers of years in periods of warming and cooling.

In Figure 2 seasonal sea-surface-temperature curves at Boothbay Harbor based on monthly mean values for each year between 1940 and 1968 are compared with the 1940-1959 mean seasonal temperature curve. As would be expected, there were marked fluctuations in the seasonal temperature cycle due to variations in runoff and meteorological conditions, but for the most part, the monthly deviations reflected the annual deviations in both periods of warming and cooling.

Similar warming and cooling trends have occurred offshore, both at the surface and at depth (Taylor, Bigelow, and Graham, 1957; Lauzier, 1965, 1967; Colton, 1968a, 1968b, 1969). Though offshore temperatures varied less seasonally than those inshore, in general, the magnitude of both surface and subsurface temperature anomalies were greater offshore than along the coast. These warming and cooling trends are associated with changes in the composition of the subsurface water (Colton, 1968b, 1969). Cold years occur when slope water is displaced or modified by coastal water of Labrador origin. Warm years occur when slope water borders upon the 200-m isobath and the ratio of coastal to central Atlantic water is low.

Taylor et al. (1957) concluded that although there was evidence of northward shifts in the abundance and distribution of some marine animals as a consequence of the warming trend which commenced in the early 1940's, these

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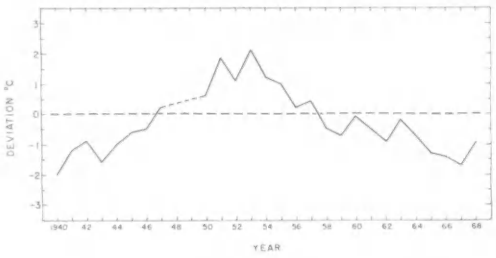

FIGURE 1.—Annual deviations from the 1940-1959 mean sea-surface temperature at Boothbay Harbor, Maine.

changes did not appear to have produced any obvious alteration of the general faunal characteristics of the Gulf of Maine. During the recent cooling period, there were a number of reports of southward extensions of range and shifts in the distribution of fish and invertebrate fauna: (1) Boyar (1964) reported the occurrence of the Greenland halibut (*Reinhardtius hippoglossoides*) off Boothbay Harbor, Maine, in February 1963. This is a southern shoal-water record for this subarctic species. (2) Substantial numbers of capelin (*Mallotus villosus*) were caught in the Bay of Fundy in the spring of 1965 (Tibbo and Humphreys, 1966) and have continued to be taken each spring through 1968 (S. N. Tibbo, personal communication). There has been no written record of the occurrence of capelin in this area since 1919 (Bigelow and Schroeder, 1953). (3) Since 1961, spiny dogfish (*Squalus acanthias*) have been collected with increasing frequency during the winter months in South Carolina coastal waters (Bearden, 1965). This species is uncommon south of Cape Lookout, N.C., and there have been no previous records of its occurrence off South Carolina. (4) Collette and MacPhee (1969) reported the collection of an arctic shanny (*Stichaeus punctatus*) in Massachusetts Bay in August 1968. This is the second record of this northern species in the Gulf of Maine and extends the known range 180 miles to the southwest. (5) Finally, the green crab (*Carcinus maenas*), which became abundant as far northeast as Nova Scotia in the mid-1950's, has declined in abundance, coincident with the decline in temperature. The green crab is now rare in Canada and eastern Maine, but still abundant in southwestern Maine and northern Massachusetts (Welch, 1968).

Such observations of northward and southward shifts in the abundance and distribution of marine animals have usually been based on sporadic observations and on commercial fishery statistics. The accumulation of records of occasional occurrences over a number of years can give the impression of a change in distribution sustained over a period of time. Many of the fluctuations in commercial fishery landings are due to changes in fishing methods, efficiency, effort, and market conditions. As Bell and Pruter (1958) have demonstrated, it is deceptively easy to infer relationships and draw false conclusions from such data. Given adequate research vessel surveys, however, it should be possible to determine the relative abundance and distribution of fish and invertebrate fauna with some precision. In this paper such otter-trawl survey data are used to determine what effect the recent cooling trend has had on the distribution of some of the important commercial species of groundfish in continental shelf waters between Nova Scotia and Long Island.

A great diversity of pelagic, hemipelagic, and demersal fish species were caught during the otter-trawl surveys. Our initial analysis was limited to the relatively abundant commercially exploited groundfish species felt to be representatively sampled by the otter trawl, e.g., those species living on or in close association with the bottom and within the depth limits covered by the surveys (approximately 30-350 m). For this study, four species were selected which represent the basic types of geographic zonation characteristic of the area. The general geographic distribution of these species is as follows:

AMERICAN PLAICE (*HIPPOGLOSSOIDES PLATESSOIDES*)

The plaice is an arctic-boreal species which is found in abundance from Greenland to Cape Cod. In the Gulf of Maine this species is most plentiful in depths ranging from 30 to 200 m.

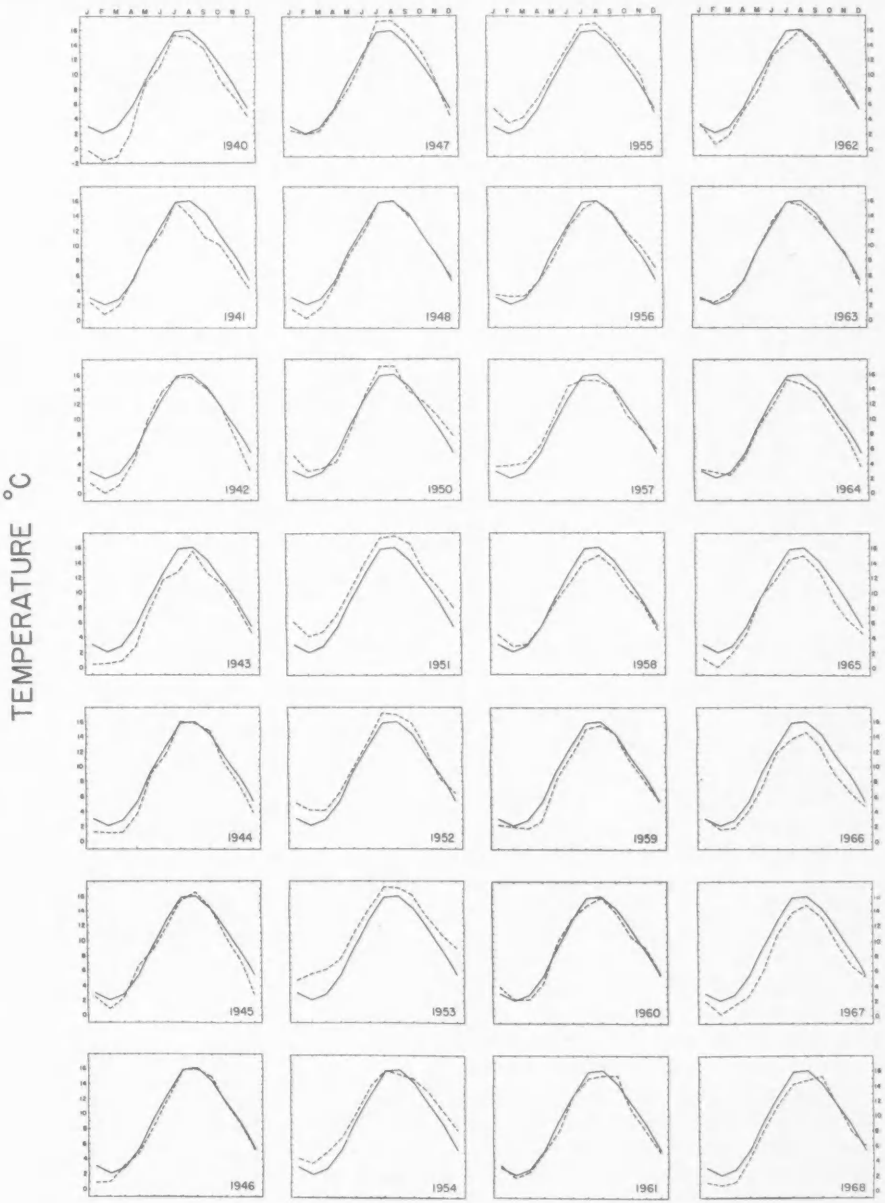

FIGURE 2.—1940-1959 mean and yearly seasonal temperature curves, Boothbay Harbor, Maine. Solid line: 1940-1959 mean, dashed line: individual year. The 1949 records are incomplete and have not been included.

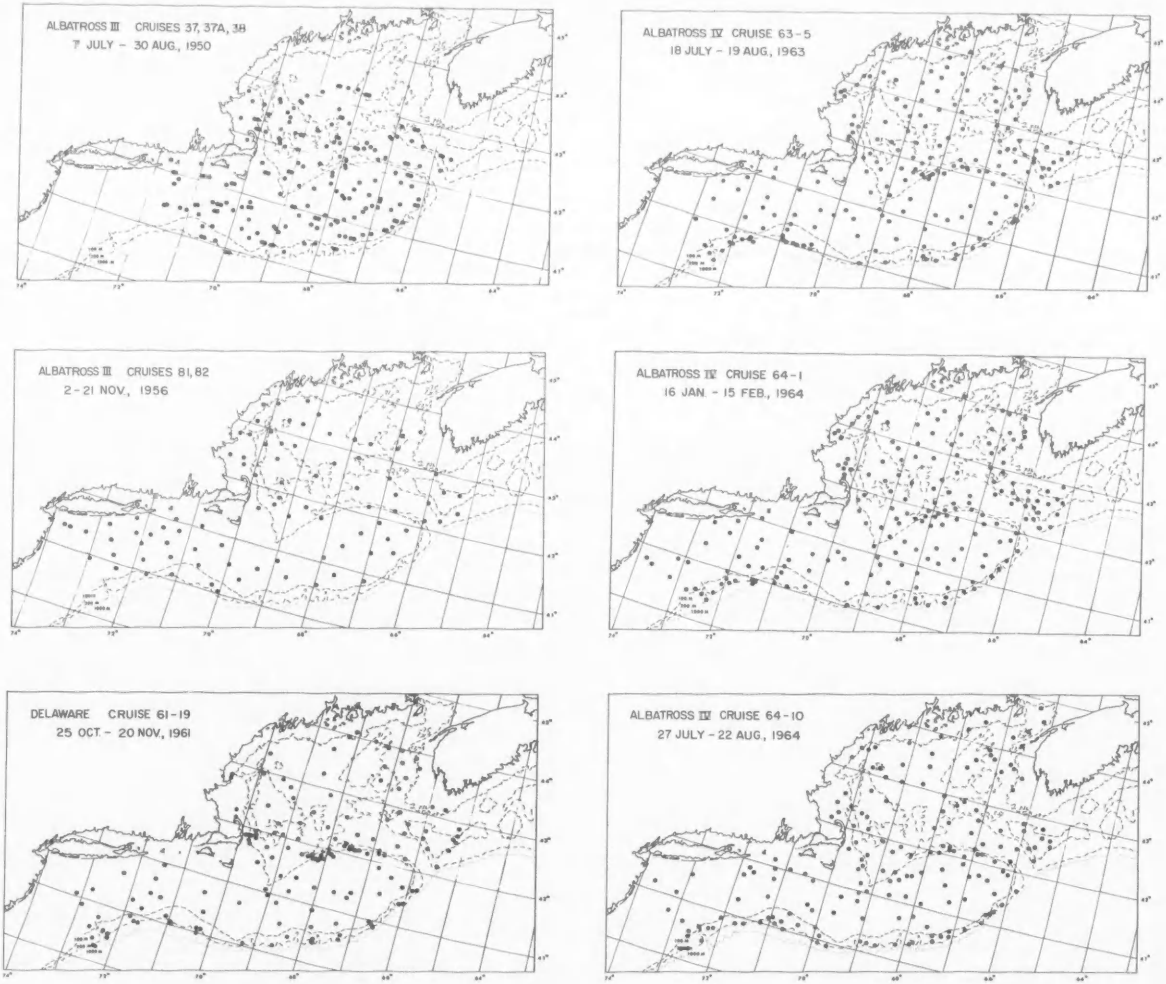
ALBATROSS III CRUISES 37, 37A, 38
7 JULY - 30 AUG., 1950
ALBATROSS IV CRUISE 63-5
18 JULY - 19 AUG., 1963
ALBATROSS III CRUISES 81, 82
2-21 NOV., 1956
ALBATROSS IV CRUISE 64-1
16 JAN. - 15 FEB., 1964
DELAWARE CRUISE 61-19
25 OCT. - 20 NOV., 1961
ALBATROSS IV CRUISE 64-10
27 JULY - 22 AUG., 1964

FIGURE 3.—Dates and station locations of groundfish cruises, July-August 1950 through July-August 1964.

Cape Cod (lat 40°30'N, long 70°00'W) marks the southern and western limits of its normal range, although plaice are occasionally taken west to Block Island. Tagging experiments in the Grand Banks area (Pitt, 1969) suggest that there are a number of relatively sedentary populations of plaice and that the limited migrations that do occur are associated with spawning and feeding patterns. Research ship and commercial catch statistics indicate that this is also true of the Gulf of Maine populations.

HADDOCK (*MELANOGRAMMUS AEGLEFINUS*)

The haddock is a boreal species inhabiting both sides of the North Atlantic whose distribution, for the most part, is confined to waters shoaler than 200 m. On the American coast the westerly limit of its normal occurrence is the Nantucket Shoals area (long 70°00'W) although in winter haddock are sometimes taken in the area between Nantucket Shoals and New Jersey. Young-of-the-year haddock are found in the area between Nantucket Shoals and Hudson Canyon during the summer and fall. Indications are that the majority of these young fish are concentrated at mid-depths (Colton, 1965) and caught while the trawl is being set out and retrieved. Young-of-the-year haddock are not included in the catch statistics presented in this paper. Tag returns and the distribution of commercial fishing effort indicate that in comparison with the cod, the haddock is a relatively stationary fish, and except for short-term shifts in depth distribution they do not follow any regular migratory routes (Needler, 1930; Schroeder, 1942; Schuck, 1952).

YELLOWTAIL FLOUNDER (*LIMANDA FERRUGINEA*)

The yellowtail flounder is a shallowwater species which occurs along the Atlantic coast of North America from Labrador to New Jersey. The bulk of the catch is taken in water shoaler than 100 m. The yellowtail flounder is one of the few species which is common both to the east and west of Cape Cod at all seasons of the year. The tagging studies of Royce, Buller, and Premetz (1955) and Lux (1963) show that, in general, the populations of New England yellowtail are to be found in relatively localized groups which may make short seasonal migrations and only a limited amount of mixing takes place between groups.

BUTTERFISH (*PEPRILUS TRIACANTHUS*)

The butterfish ranges in the northwestern Atlantic from the outer coast of Nova Scotia and Cape Breton to northern Florida. There is a separate population in the Gulf of Mexico (Caldwell, 1961). This temperate-region species is only a warm season migrant to coastal waters off New England and the Maritime Provinces. In general, butterfish appear off southern New England at the end of April, but it is not until July that they are plentiful in the inner parts of the Gulf of Maine and on Georges Bank. Butterfish disappear from the coast by the end of December at the latest.

COLLECTION AND REDUCTION OF DATA

The data were collected during the period 1950-1968 by personnel at the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) Biological Laboratory, Woods Hole, Mass., on surveys designed to determine the distribution and relative abundance of groundfish in the Gulf of Maine and adjacent waters. The fishing gear used during these surveys was similar to that being used by the commercial haddock fleet at the time. A 1½ Iceland trawl was used prior to 1951, and a No. 36 redfish trawl has been used since that time. A description of these trawl nets is given by Knake (1956). The cod end and top belly of both type nets were lined with fine mesh netting to retain smaller fish. Three vessels were used in these surveys; the side trawlers *Albatross III* and *Delaware* and the stern trawler *Albatross IV*. On all cruises the trawl was towed for 30 min at each station at a vessel speed of approximately 3.5 knots. Various sampling patterns employing both random and grid station

FIGURE 3.—Dates and station locations of groundfish cruises, July-August 1968 through July-August 1968.

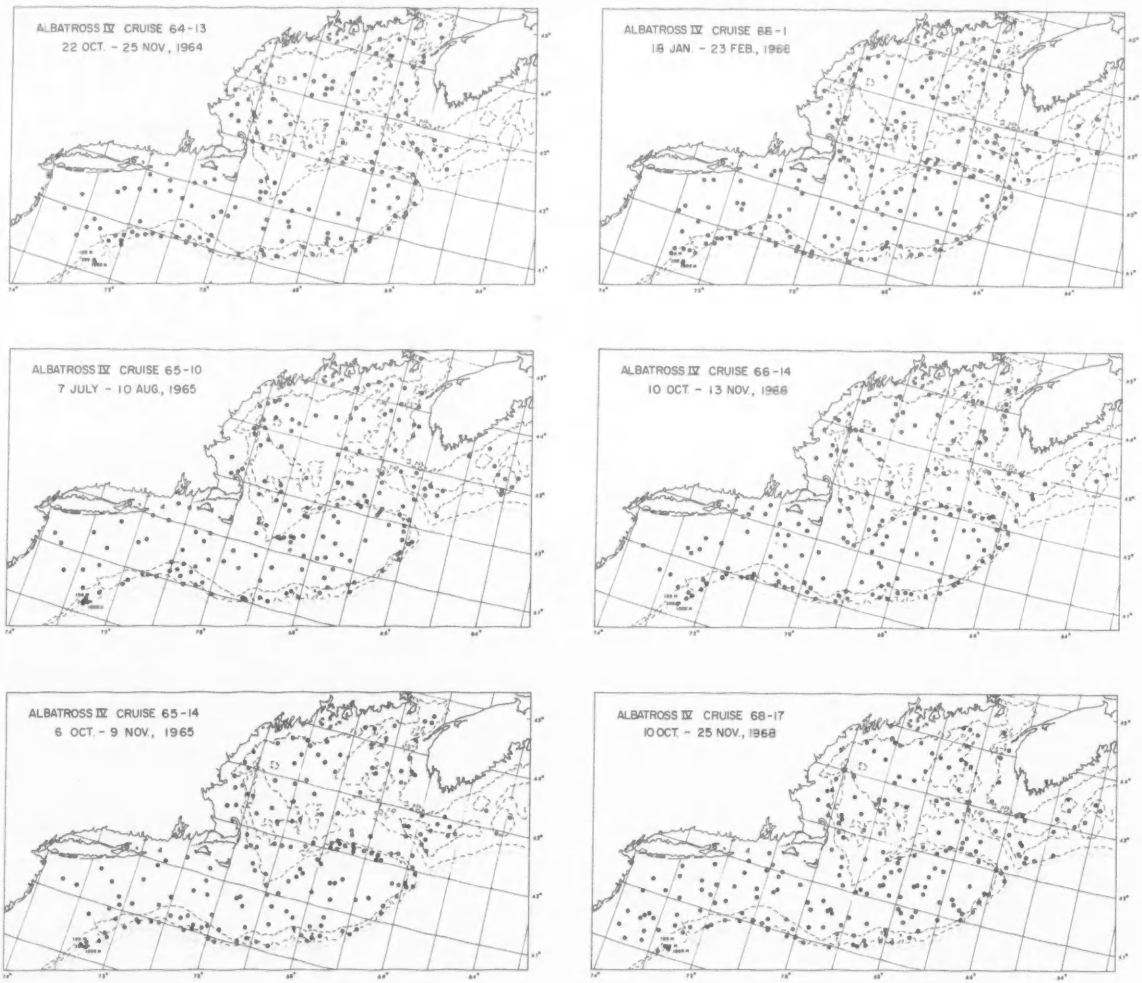
ALBATROSS IV CRUISE 64-13
22 OCT. - 25 NOV., 1964
ALBATROSS IV CRUISE 65-1
18 JAN. - 23 FEB., 1965
ALBATROSS IV CRUISE 65-10
7 JULY - 10 AUG., 1965
ALBATROSS IV CRUISE 66-14
10 OCT. - 13 NOV., 1966
ALBATROSS IV CRUISE 65-14
6 OCT. - 9 NOV., 1965
ALBATROSS IV CRUISE 68-17
10 OCT. - 25 NOV., 1968

FIGURE 4.—Dates and station locations of groundfish cruises, October-November 1964 through October-November 1968.

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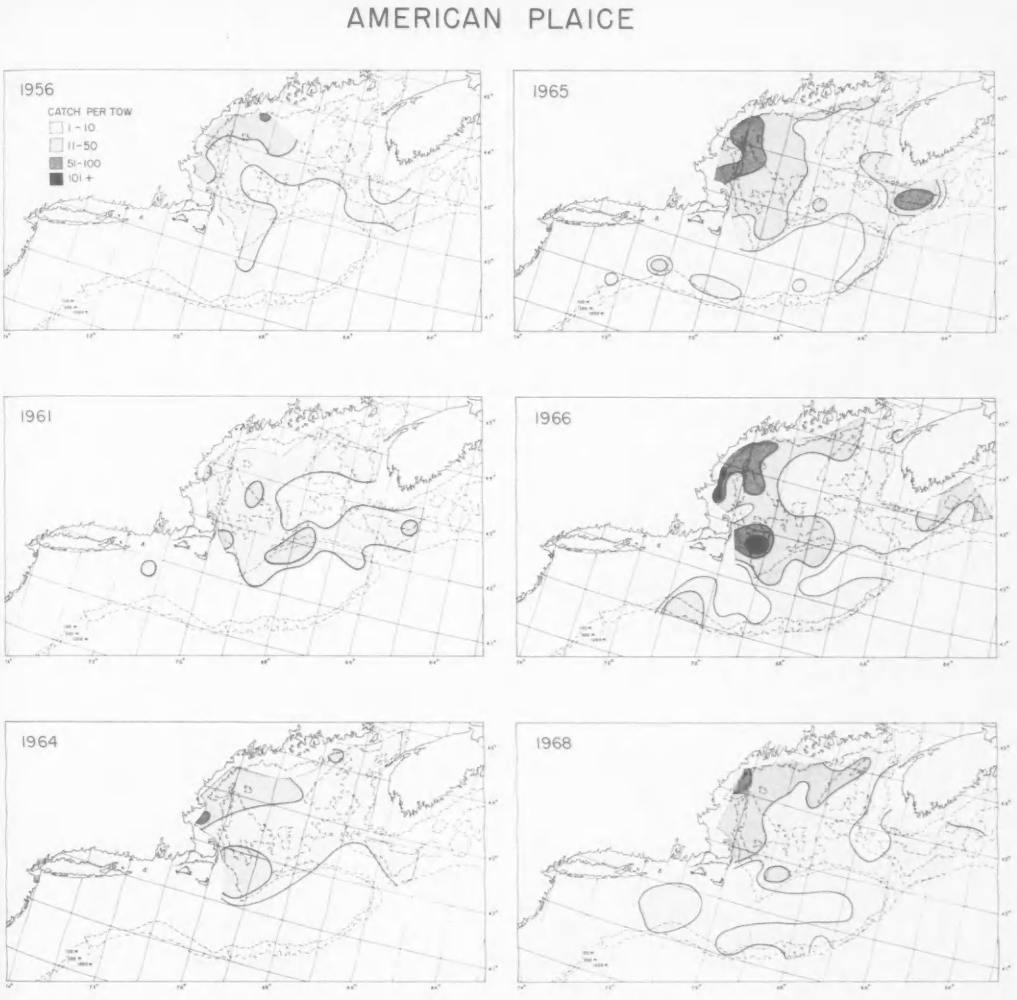

FIGURE 5.—Distribution of American plaice during October-November.

FIGURE 4.—Dates and station locations of groundfish cruises, October-November 1964 through October-November 1968.

designs were used, but for most cruises a stratified random sampling technique was employed in which station location and number were prorated by area and depth zone. A complete description of the sampling design currently being employed is given by Grosslein (1969).

Although an effort was made to standardize sampling techniques, comparative tows made with the *Albatross III* and the *Delaware* and the *Albatross IV* and the *Delaware* showed that fishing efficiency varied to some extent between vessels and with towing methods (stern vs. side trawling). Fishing efficiency also varies with time of day and with species and age of fish (Bigelow and Schroeder, 1953; Colton, 1965; Fritz, 1965). However, for the purpose of de-

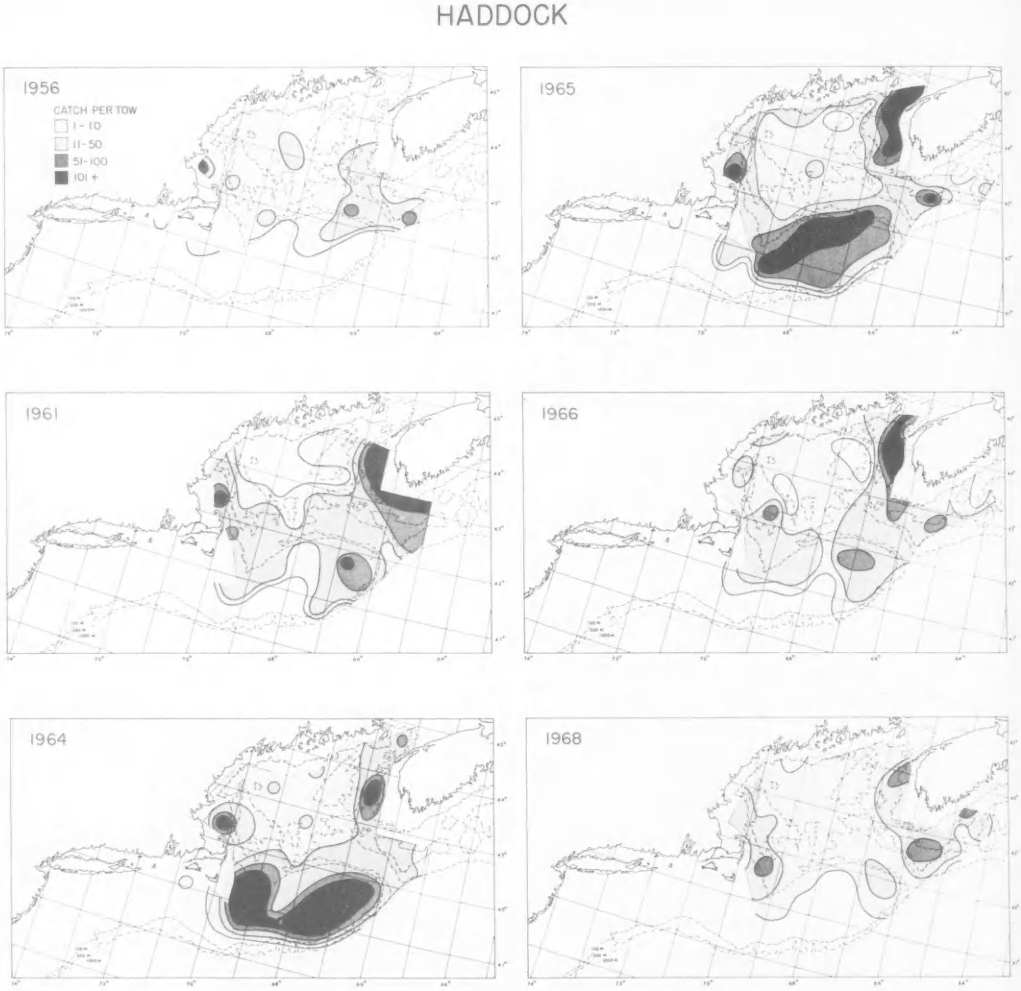

FIGURE 6.—Distribution of haddock during October-November.

lineating the general distribution patterns of the species of fish considered in this paper, the survey data would appear to be adequate.

For most species and in most areas there were marked differences in the catch at adjacent stations. In preparing the species distribution charts, the average number of fish per tow for all stations lying within 30″ latitude and longitude quadrangle areas was determined. The contour lines were drawn on a basis of these average values entered at the center of each 30″ quadrangle. Considerable smoothing and interpolation were still necessary, especially in cases where the bathymetry required adjustments in order to avoid contouring a species outside its normal depth range as indicated by individual

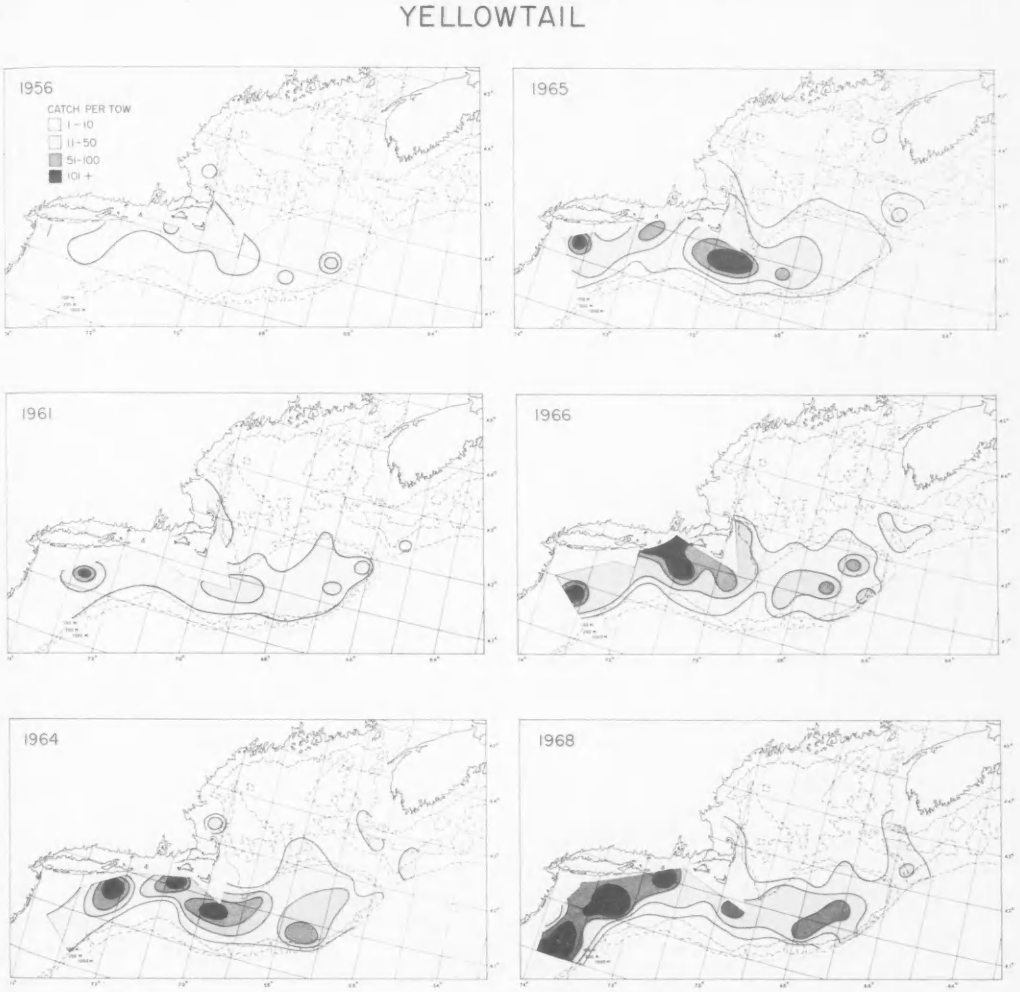

FIGURE 7.—Distribution of yellowtail flounder during October-November.

station data.

Groundfish surveys were conducted principally during the fall months in an effort to estimate the strength of new year classes of haddock, but some surveys were made at other seasons of the year. There was considerable yearly variation between cruise dates during any one season. In order to eliminate the effects of short-term shifts in distribution, only cruises spanning approximately similar time periods were used in comparing yearly distribution patterns. The dates and trawl station locations of the cruises considered in this paper are shown in Figures 3 and 4.

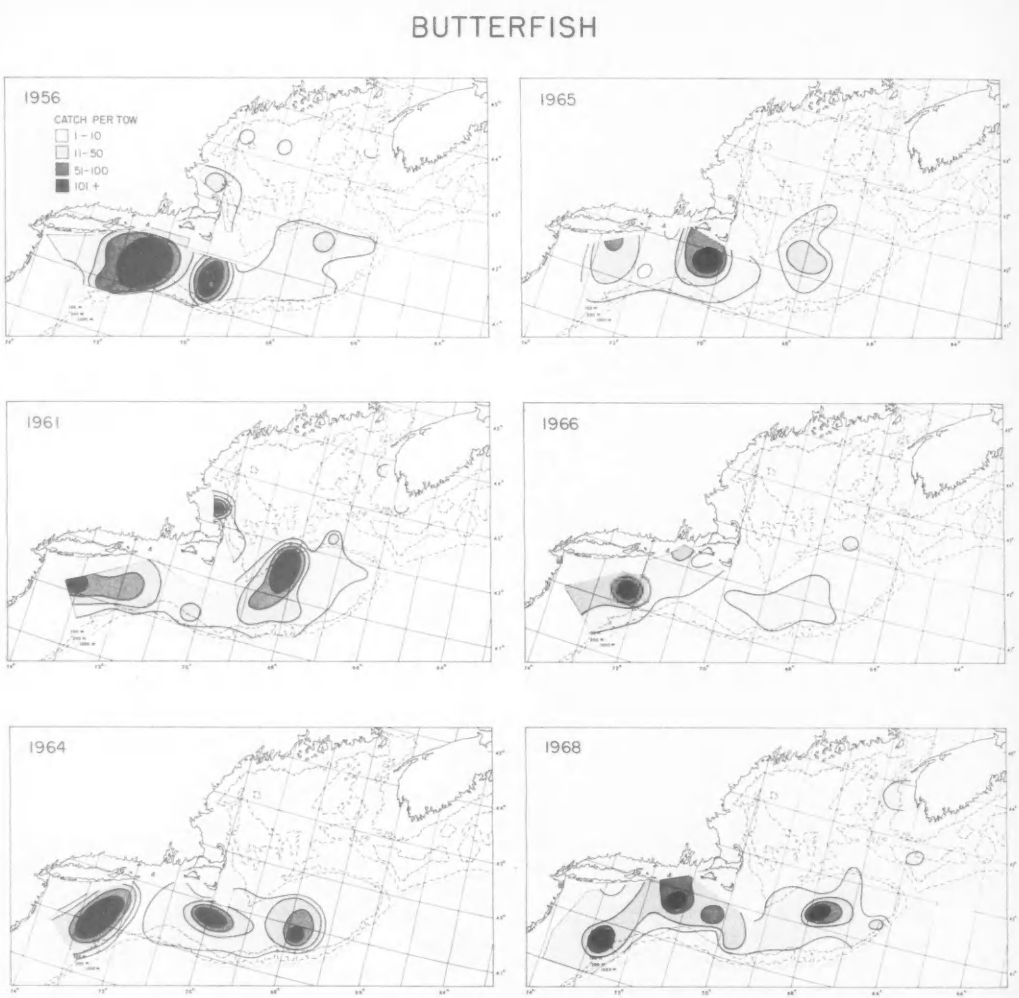

FIGURE 8.—Distribution of butterfish during October-November.

OCTOBER-NOVEMBER DISTRIBUTION

The distribution of American plaice, haddock, yellowtail flounder, and butterfish during October-November 1956, 1961, 1964, 1965, 1966, and 1968 is shown in Figures 5-8.

During 1956, 1961, and 1964, the catches of American plaice were confined to the area north of lat 41°N and east of Cape Cod. In 1965, 1966, and 1968, plaice were found over a much more extensive area. In these years plaice occurred along the southern edge of Georges Bank and off southern New England as far west as long 72°W. The abundance of plaice, as indicated by the average catch per tow, was greater during the latter 3 years.

The catches of haddock were confined to the area east of Nantucket Shoals (long 70°W). The general distribution pattern was similar during all years with the exception that in 1956 (the warmest year) the southern limit of occurrence of haddock was north of its position during the other years. For the most part, the variations in abundance and distribution of haddock between years appear to be related to changes in age composition of the catch due to the predominance of certain year classes. For example, the catches during 1964 and 1965 consisted principally of 1- and 2-year-old fish of the strong 1963 year class (Grosslein, 1969). In general, these young haddock inhabit shoaler water than do older haddock (Colton, 1955).

Although there were marked fluctuations in the abundance of yellowtail flounder between years, there was little change in the general distribution pattern. In all years yellowtail were found in relatively shoal water (<100 m) both to the east and west of Cape Cod. With the possible exception of 1956, the distribution of yellowtail extended considerably beyond the western limit of the sampling area. The bulk of the catch was made south of lat 42°N, although small concentrations occurred off the tip of Cape Cod and on Browns Bank. The greater abundance of yellowtail in later years appears to be due to a succession of strong year classes and not to a major shift in distribution (Lux, 1969).

The main concentrations of butterfish occurred on western Georges Bank and Nantucket Shoals and off southern New England and Long Island. As in the case of the yellowtail, the distribution of butterfish extended beyond the western limit of the sampling area. In 1956 and 1961 only, appreciable numbers of butterfish were caught north of lat 42°N. In these years butterfish occurred just east of Cape Cod, in the Stellwagen Bank area, and in scattered concentrations within the Gulf of Maine. Butterfish were least abundant in 1966. In this, the coldest year, few fish were taken east of Nantucket Shoals.

JULY-AUGUST DISTRIBUTION

The distribution of American plaice, haddock, yellowtail flounder, and butterfish during July-August 1950, 1963, 1964, and 1965 is shown in Figures 9 and 10.

The area of occurrence of plaice extended farther south and west with succeeding years and decreasing temperatures. The catches of haddock were confined for the most part to the area east of Nantucket Shoals, and there was little change in distribution between years. The similarity of the distribution patterns of haddock during July-August and October-November 1964 and 1965 indicates limited seasonal movement. Little change was evident in the general distribution patterns of yellowtail between years. As in the case of the haddock, the similarity of the distribution patterns during July-August and October-November 1964 and 1965 indicates little seasonal movement. There were no marked differences in the distribution of butterfish in these years, although butterfish were least abundant on Georges Bank in 1965, and 1950 was the only year in which appreciable numbers were taken in Cape Cod Bay. In contrast to October-November, the distribution of butterfish during July-August 1964 and 1965 was confined within the western limits of the sampling area.

SEASONAL DISTRIBUTION

Of the four species considered in this paper, only the American plaice and the butterfish showed any appreciable change in distribution coincident with the downward trend in temperature. During both summer and fall there was an extension of the southern and western limits of the area of occurrence of plaice and a contraction of the northern and eastern limits of the area of occurrence of butterfish. Data obtained on cruises made during January-February 1964 and 1966, together with data collected during July-August and October-November 1964 and 1965 (Figures 11 and 12), give evidence of the seasonal distribution of these two species.

Although there were no extensive seasonal changes in the distribution of plaice, the southwesterly extent of the distribution boundaries tended to be greatest during January-February and least during October-November (Figure

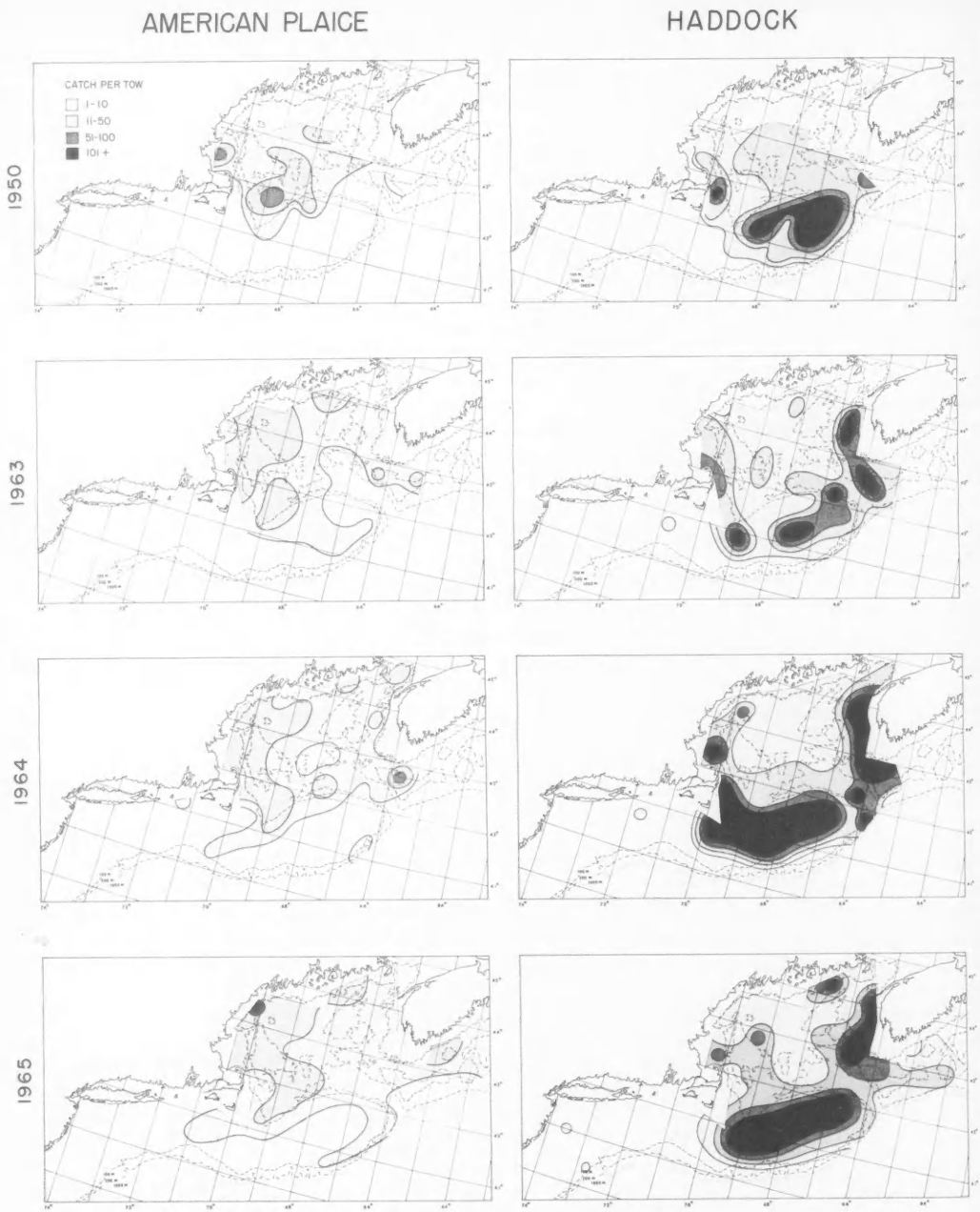

FIGURE 9.—Distribution of American plaice and haddock during July-August.

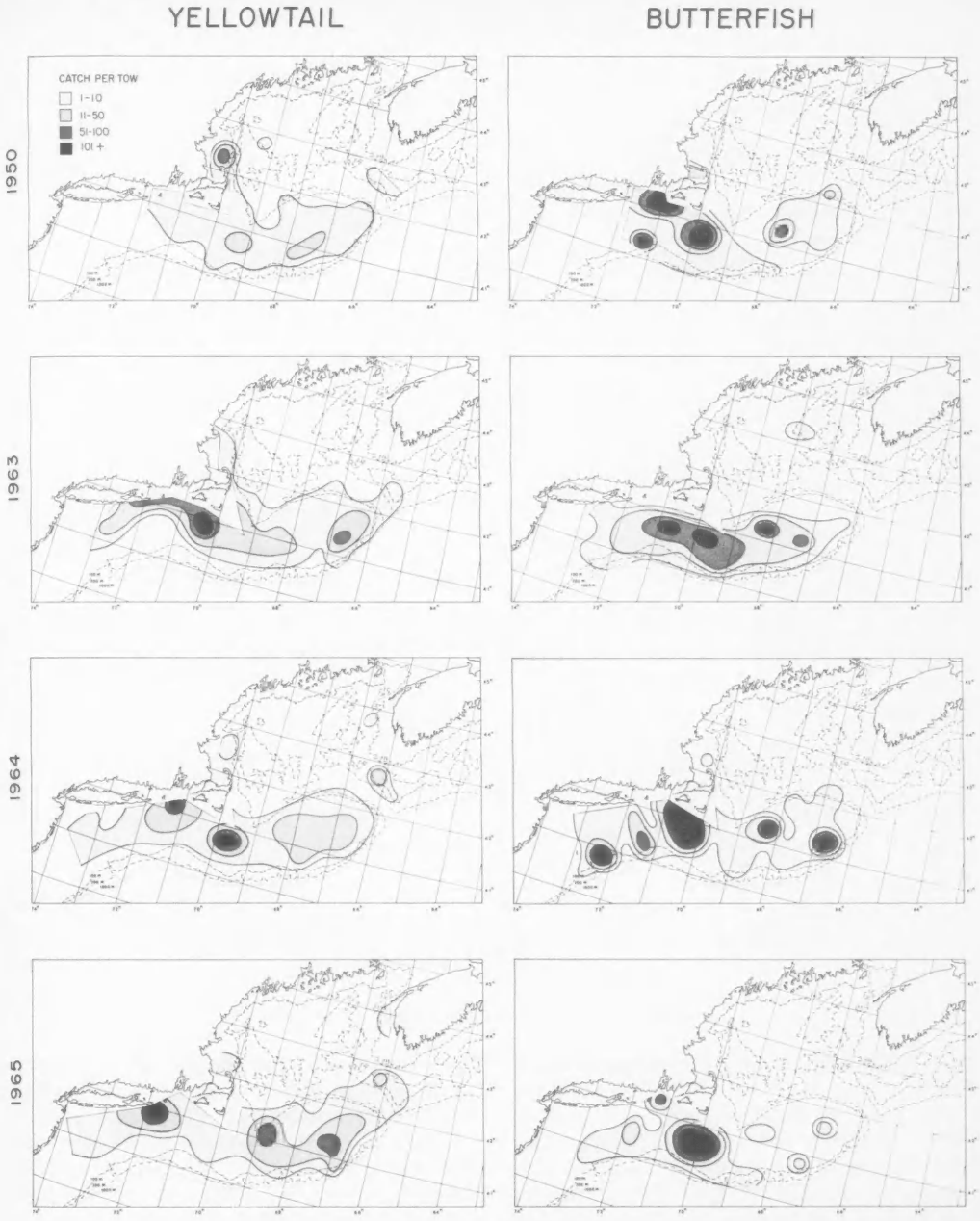

FIGURE 10.—Distribution of yellowtail flounder and butterfish during July-August.

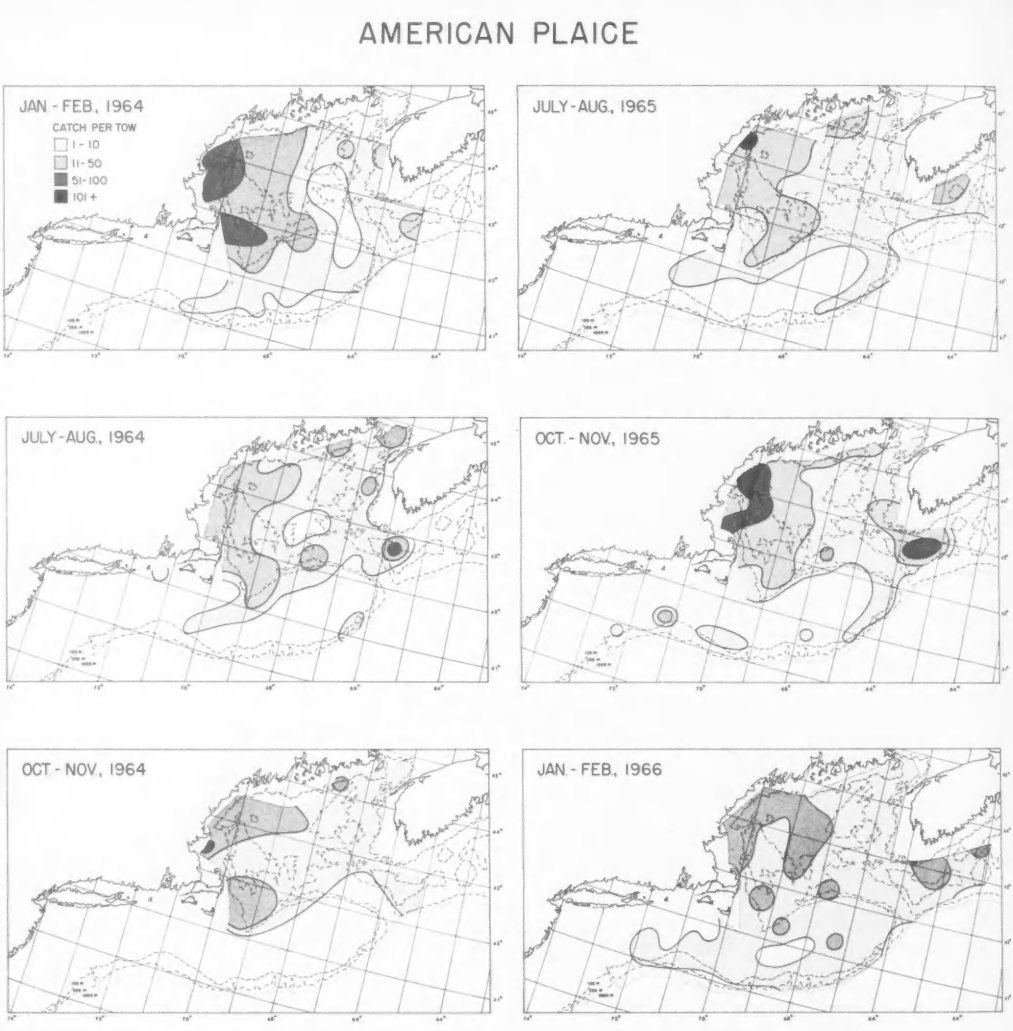

FIGURE 11.—Seasonal distribution of American plaice.

11). In addition, it was only during January-February that plaice were caught in the shoal-water areas of Georges Bank. This seasonal shift in distribution appears to be associated with temperature change. The seasonal maximum and minimum bottom-water temperatures at the depths most frequented by plaice (30-200 m) occur during October-November and February-March respectively (Colton, 1968a; Colton and Stoddard, In press). Bottom-water temperatures over the shoal-water areas of Georges Bank are appreciably higher than those along its periphery during the summer and fall while in the winter and spring the reverse situation exists.

There were no appreciable changes in the dis-

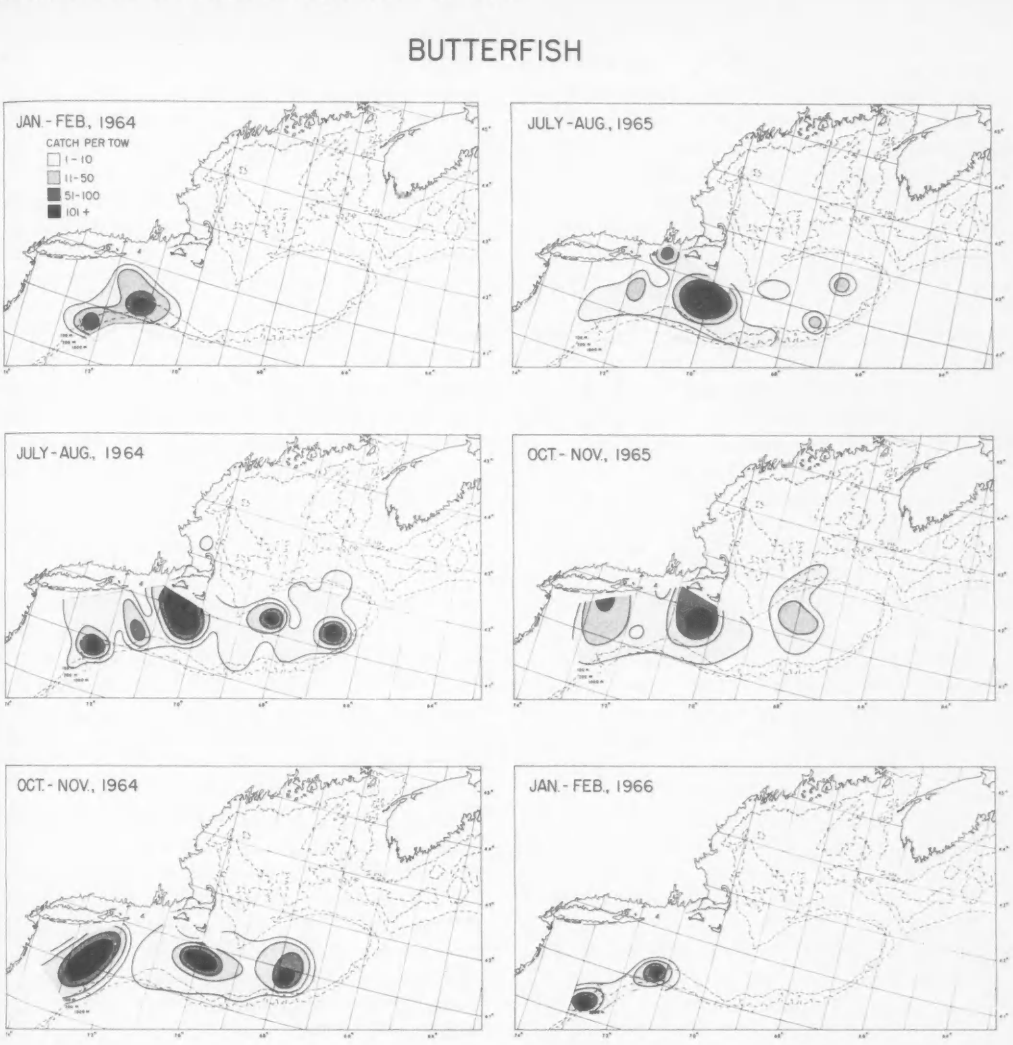

FIGURE 12.—Seasonal distribution of butterfish.

tribution of butterfish between July-August and October-November (Figure 12). However, the fact that the distribution during October-November extended beyond the western limits of the sampling area indicates that butterfish begin their offshore migration from New England coastal waters at this time. By January-February the offshore migration was completed and butterfish were only found in deep water in the southwest corner of the sampling area.

DISCUSSION

A seasonal cold-water temperature barrier in the region of Cape Cod and Nantucket Shoals separates the coastal waters of the Gulf of Maine and the Middle Atlantic Bight from the end of

June to the end of September (Bigelow, 1927; Parr, 1933). This barrier is marked by the presence of a surface pool of cold upwelled water. At other seasons of the year there is open continuity between coastal temperature conditions north and south of Cape Cod. This temperature barrier coincides with the poleward and equatorward boundaries of many species of marine fauna, both pelagic and benthic (Bigelow and Sears, 1939; Parker, 1948; Fritz, 1965; Schopf, 1965).

The seasonal ranges of surface- and bottom-water temperatures in most areas within the Gulf of Maine are less extreme than those characteristic of the Middle Atlantic Bight. The seasonal range of temperature in the shoal-water area of Georges Bank, however, is as great as that at similar depths in the area between Nantucket Shoals and New Jersey (Colton and Stoddard, 1972 and In press). Parr (1933) has described the ecological relationships between homothermal and heterothermal regions separated by a seasonal temperature barrier and has discussed the effect that these contrasting temperature regimes have on the period, extent, and character of the migratory activities of shallow-water fish populations. There is a marked seasonal alternation in the composition of the fish fauna of the Middle Atlantic Bight. In summer this area contains a very rich population of southern migratory fishes which follow the northward dispersal of isotherms as far north as Cape Cod. Winter temperature conditions compel this population to vacate the area, and it is replaced to a considerable extent by northern species, such as herring and cod, which at this season have free access to penetrate as far south as the neighborhood of Cape Hatteras. Although there is no thermal barrier during the winter, the qualitative composition of the fish fauna is not uniform from north to south around Cape Cod. As Parr (1933) has pointed out, this seasonal diffusion of northern populations into areas where no significant temperature differences exist is distinguishable in both its character and effects from the northerly and southerly migrations of complete populations such as occur under thermal compulsion within the Middle Atlantic Bight. In contrast to the Middle Atlantic Bight which contains very few permanent residents, the bulk of the fish fauna in the Gulf of Maine are endemic to the area and there is little seasonal alternation in species composition.

Hutchins (1947) recognized four basic types of temperature zonation which depend on maximum and minimum temperatures critical for survival and repopulation. With the exception of estuarine species such as the green crab which may be subject to winter kill, the distribution of benthic organisms in the area off New England appears to be controlled by summer rather than winter temperatures (Hutchins, 1947; Schopf, 1967). The equatorward boundary of potentially southward-migratory forms is limited by summer temperatures too high for survival and the poleward boundary of northward-migratory forms by summer temperatures too low for reproduction (type 3 of Hutchins, 1947). This is in agreement with the assumption of Hutchins (1947) that at localities having a temperature barrier at only one season (summer at Cape Cod), all distributions terminating there are associated with that barrier.

It is difficult to categorize fish species by strict temperature zonation characteristics. Fish do not have built-in integrators and so must react to prevailing rather than to average conditions. Unlike many benthic invertebrates, fish are able to make short-term excursions and are not dependent solely on passive migrations. It should also be stressed that the distribution within the broad limits set by temperature extremes for survival and reproduction is controlled to some extent by other factors such as food supply (Blackburn, 1969) and substrate conditions (Bigelow and Schroeder, 1953). Of the species considered in this paper, only the American plaice and the butterfish exhibited the expected response to cooling, e.g., extension of the southern range of northern endemic forms and diminution of the northern range of southern migrants.

The butterfish is the only species considered which shows a sensitivity to small changes in temperature and which migrates under the thermal compulsion. Ripe butterfish are taken

throughout their entire range (Caldwell, 1961). In the Gulf of Maine spawning occurs from June through August (Bigelow and Schroeder, 1953). In general, the first arrivals at any point along the coast are in spawning condition, and it would appear that the summer poleward boundary is governed by the minimum temperature suitable for reproduction. Although one can only generalize as to temperature dependence, the timing of arrival of butterfish at various points along the coast of New England and the Maritime Provinces suggests that the minimum spawning temperature is approximately 15°C. The time at which butterfish leave the coastal waters and their distribution in deep water along the continental slope during the winter months indicate a minimum temperature for survival of about 10°C. These temperature approximations are based on average values given by Colton and Stoddard (1972 and In press).

Bigelow and Schroeder (1953) state that the American plaice spawns throughout the Gulf of Maine, but principally in water shoaler than 100 m. More recent observations (Marak and Colton, 1961; Marak, Colton, and Foster, 1962; Marak, Colton, Foster, and Miller, 1962) confirm that the plaice has no well-defined spawning area, although plaice eggs were most abundant in the western Gulf of Maine and over the southeastern part of Georges Bank. Plaice spawn from March through May (Bigelow and Schroeder, 1953). Long-term temperature data in the areas of maximum spawning (Colton and Stoddard, In press) suggest an optimum spawning temperature of 3°-6°C. During the spawning period such bottom-water temperature conditions prevail over most of the area within the 100-m isobath from Cape Cod to New Jersey. Thus, the equatorward boundary of plaice appears to be limited by summer and fall temperatures too high for survival rather than temperatures during the spawning season that are too high for reproduction. As noted previously, plaice were not caught in the Georges Shoal area during the summer and fall. The long-term temperature distribution in this area indicates a maximum temperature for survival of about 12°C. Bigelow and Schroeder (1953) give a range of 10°-13°C as the upper limit of regular occurrence of American plaice.

In contrast to the American plaice, the spawning of haddock is restricted to limited areas within the Gulf of Maine. The most productive spawning grounds are in depths ranging from 40 to 100 m on the northeastern part of Georges Bank and on Browns Bank (Walford, 1938; Bigelow and Schroeder, 1953; Colton and Temple, 1961). Limited and less consistent spawning occurs in the South Channel, Stellwagen Bank, and Jeffreys Ledge areas. Haddock spawn from February through May with the height of spawning occurring on Georges Bank during March and April and on Browns Bank during April and May. Long-term temperature data in the areas of maximum spawning suggest an optimum spawning temperature of 4°-6°C, although spawning does take place at temperatures below and above this range (2°-7°C). There is no evidence that haddock spawn west of Cape Cod, although favorable temperature conditions exist over most of this area during the spawning season.

It is not apparent why haddock select restricted spawning areas, but this limitation may govern in part the extent of their seasonal diffusion into waters west of Cape Cod. Bigelow and Schroeder (1953) give 11°C as the upper temperature limit of the normal range of occurrence of haddock, but the fact that haddock are caught in the Georges Shoal area during the warmest part of the year indicates that haddock can survive temperatures at least as high as 15°C for limited periods. Bottom-water temperatures well below this upper limit occur over much of the area between Cape Cod and Long Island during the summer and fall.

Although seasonal shifts in depth distribution and the timing of spawning of haddock appear to be regulated in part by temperature (Bigelow and Schroeder, 1953; Colton, 1968a), the fact that there was no appreciable change in the geographic distribution of haddock coincident with the downward trend in temperature suggests that factors other than temperature are also critical in the geographic zonation of this species. Bigelow and Schroeder (1953) note that haddock are selective as to substrate type. Haddock avoid areas of rock, kelp, and exceptionally

soft mud and are chiefly caught over broken ground, gravel, pebbles, clay, and smooth hard sand. However, there are no conspicuous differences in the sediments of the Continental shelf east and west of Nantucket Shoals (Uchupi, 1963). Sediments on Georges Bank consist of coarse sand and scattered patches of gravel. In the area between Nantucket Shoals and Hudson Canyon, there is a nearshore zone of silty sand and sandy silt and scattered patches of gravel. Between the 30- and 60-m isobaths is a zone of coarse sand and scattered patches of gravel. From the 60-m isobath to the edge of the shelf, the sediments are similar to those in the basins of the Gulf of Maine and consist of silty sand, sandy silt, and silt.

On a basis of a stomach content analysis of haddock collected on Georges Bank during 1953-54, Wigley (1956) concluded that haddock are exceedingly omnivorous. Their diet consisted principally of sedentary or slow-moving invertebrate animals. The primary food organisms in decreasing order of abundance were crustaceans, mollusks, echinoderms, annelids, and fish. There was considerable variation in dietary components from one location to another. Having no supplementary data on the distribution of benthic fauna, it could not be determined if this variation in diet was related to faunal composition. More recent studies of the distribution of benthic fauna on the continental shelf between Nova Scotia and Long Island (Wigley, 1961; Wigley and McIntyre, 1964; R. L. Wigley—personal communication) show that haddock prefer crustaceans to other food organisms and that the quality and quantity of the benthic fauna to the west of Nantucket Shoals are more than adequate to support a large population of haddock. It is possible that competition for food by the very rich summer and fall populations of such species as the spiny dogfish, silver hake (*Merluccius bilinearis*), and red hake (*Urophycis chuss*) is a factor in restricting the haddock from the Middle Atlantic Bight.

As mentioned previously, the yellowtail flounder is common both to the east and west of Cape Cod at all seasons of the year. Bigelow and Schroeder (1953) observed that the restricted depth range and the nonmigratory habit of this species indicate that yellowtail can tolerate a wide range of temperature. This eurythermic tolerance is further evidenced by the long spawning season and extensive spawning area of this species. The yellowtail breeds over its entire range and from March through August. The spawning period appears to be no later east of Cape Cod than to the west. In addition, Bigelow and Schroeder (1953) noted that individual females evidently spawn over a considerable period of time for only a small part of the eggs ripen simultaneously. The above authors estimated that the yellowtail was subject to a range of temperature from season to season in one part of its area of occurrence or another from about 1° to 12°C. However, the distribution of yellowtail off southern New England and Long Island during the warmest part of the year indicates that they can tolerate temperatures at least as high as 16°C for limited periods.

Yellowtail flounder are only found over sand and sand-mud bottoms and never over rocks, stony ground, and very soft bottom (Bigelow and Schroeder, 1953). This preference for sand sediments is especially evident if one compares the distribution of yellowtail shown in Figures 7 and 10 with the distribution of sediment type shown by Uchupi (1963, Figure 94.1). This predilection for sand sediments is also shown in the data of Fritz (1965, Plates B and 14). It would appear then that except at the extreme northerly and southerly limits of its range, the geographic distribution of yellowtail is more strongly influenced by bottom type than by temperature.

It is possible that changes in distribution occurred which were not evident from the survey data due to limitations of sampling and analysis. For example, a number of groundfish species inhabit areas shoaler than that covered by the surveys (<30 m). Among such species is the summer flounder (*Paralichthys dentatus*), which is representative of species restricted for the most part to the area southwest of Cape Cod at all seasons of the year. Pelagic species such as menhaden (*Brevoortia tyrannus*), a warm season migrant having wide fluctuations of occurrence in the Gulf of Maine, and herring (*Clupea harengus harengus*), a boreal species

which ranges as far south as Cape Hatteras in the winter, were not representatively sampled by the otter trawl. Studies undertaken on the distribution of tunas (Blackburn, 1965, 1969) indicate that, in general, pelagic species are much more sensitive to temperature than groundfish species.

There is some evidence to the effect that sensitivity to temperature varies with age of fish. Rollefsen (1949) noted that immature cod can tolerate lower temperatures than mature cod. It is only during the spawning season that appreciable numbers of the older year classes of haddock are caught on Georges Bank (Colton, 1955). In summer these older fish move off into deeper and cooler water, and the Georges Bank population is made up principally of the younger year classes of haddock (1- to 3-year-olds). It would appear that young haddock can withstand higher temperatures than older haddock. The fact that we grouped all age fish in this study may have concealed shifts in distribution associated with specific age-groups.

Any attempt to relate geographic distribution to the direct result of physical processes involves gross oversimplification. It is apparent, however, that there was no major change in the distribution of groundfish coincident with the cooling trend, i.e., the establishment of resident populations south of Cape Cod of species that were formerly winter migrants or a northern diminution of the range of southern migrants. It would appear that the magnitude and rate of temperature change were not sufficient to significantly alter the groundfish composition in the area between Nova Scotia and Long Island. A similar conclusion was reached by Taylor et al. (1957) in their study of changes in the distribution and abundance of marine animals in the same area during a period of warming.

SUMMARY

An alternation in seawater temperature has been observed in coastal and offshore waters in the area between Nova Scotia and Cape Hatteras. There have been a number of reports of southward extensions of range and shifts in distribution of fish and invertebrate fauna during the cooling trend which commenced during 1952-53.

Research vessel survey data is presented to determine what effect the cooling trend has had on the distribution of some important commercial groundfish species in continental shelf waters between Nova Scotia and Long Island. Four species representative of the basic types of geographic zonation characteristic of the area are considered in this paper: American plaice, haddock, yellowtail flounder, and butterfish.

The American plaice and the butterfish showed a change in distribution coincident with the downward trend in temperature, but these shifts were not extensive. During both summer and fall there was an extension of the southern and western limits of the area of occurrence of American plaice and a contraction of the northern and eastern limits of the area of occurrence of butterfish. The equatorward boundary of plaice appears to be limited by summer temperatures too high for survival and the poleward boundary of butterfish by summer temperatures too low for reproduction.

There was no change in the general distribution of haddock and yellowtail flounder. In all years and seasons the catches of haddock were confined for the most part to the area east of Cape Cod. Restricted spawning areas and competition for food may govern, in part, the seasonal diffusion of haddock into waters west of Cape Cod.

Yellowtail flounder occurred both to the east and west of Cape Cod at all seasons. Their distribution was limited to depths shoaler than 100 m and to areas of sand bottom. The restricted depth range, long spawning season, extensive spawning area, and nonmigratory habit of the yellowtail flounder indicate that this species can tolerate a wide range of temperature. It appears that except at the extreme northerly and southerly limits of its range, the geographic distribution of yellowtail flounder is more influenced by bottom type than by temperature.

Although it is possible that changes in distribution did occur which were not evident from the survey data, it appears that the magnitude and rate of temperature change during the cooling period were not sufficient to significantly

alter the distribution of groundfish in the area between Nova Scotia and Long Island.

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WATER TEMPERATURE AND THE MIGRATIONS OF AMERICAN SHAD

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ABSTRACT

The peak of spawning runs of American shad (*Alosa sapidissima*) into rivers at various latitudes on the Atlantic and Pacific coasts of North America takes place when water temperatures are near 18.5°C. At the Bonneville Dam, Columbia River, Wash., 90% of the run as a rule takes place when river temperatures are between 16.0° and 19.5°C. At the fish ladder of the Holyoke Water Power Company on the Connecticut River, the temperature at the peak of the shad run averaged 19.5°C for 15 years. In the St. Johns River, Fla., peak movement occurs in December and January at the time of the annual minimum water temperatures, or 14.0° to 20.0°C.

Migrations of shad in the Atlantic Ocean follow paths associated with approximately the same range of temperatures (13.0°-18.0°C). Annual cycles of ocean warming cause shad to move into the Gulf of Maine in the summer, to the middle Atlantic in the winter, and to the south in the early spring. Juvenile shad move downstream in the fall, coinciding with a decline in the temperature of each stream to below 15.5°C. A path of migration for shad in the Pacific Ocean is hypothesized from the known seasonal changes in ocean temperature. The potential effects of artificial warming of streams on timing and survival of shad runs in northern and southern latitudes is discussed.

The American shad (*Alosa sapidissima*), in spite of declines in abundance on the Atlantic coast of the United States caused by obstruction of spawning runs by dams, by water pollution, and by overfishing, continues to provide a catch each year of some 8 million pounds valued at slightly more than one million dollars to the fishermen (Walburg and Nichols, 1967).

There is as yet no rationally based management scheme to prevent overfishing of shad, and dams and pollution continue to increase. Recent changes in the environment for shad have been brought about by the greatly increased heating of the water by steam-electric generating stations. There will be a further increase in the construction of these facilities; thus the Federal Power Commission in 1960 estimated that by 1980 the generating capacity of hydroelectric power stations would double—some accomplished by construction of dams and some by adding capacity at existing dams—but at the same time, steam-electric capacity would triple (Federal Power Commission, 1960). Other experts regard these estimates as conservative (American Public Power Association, 1960). It therefore becomes pertinent to ask what effects the warming of water may have on fish in streams used for cooling. This paper analyzes the effect of water temperature on the movements of shad in streams and in the ocean.

It is appropriate that this paper, which traces the relationship of migrations of American shad to temperature of the water, should appear in a volume dedicated to Dr. O. Elton Sette. His interest in the effects of temperature on migrations of fishes has been a stimulus to the work of his colleagues for over 30 years. He has always been generous in his encouragement of those around him. In 1957, the Pacific Oceanic Fishery Investigations, of which he was the first Director, began publication of monthly sea-surface temperature charts for the Pacific Ocean as an aid to fishermen and biologists studying fish distribution. The successors of these charts are still being issued by the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla Laboratory. Other scientists and agencies have come to see their utility and popularity and have commenced publication of sea surface temperature charts for other parts of the world.

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The present paper, therefore, owes a great deal to Dr. Sette both in its conception and execution. He conceived that there was a relationship between water temperature and fish distribution, and he stimulated the production of charts to which we are able to refer in order to establish the relationship of shad migrations to water temperature.

SHAD RUNS AND RIVER TEMPERATURE

As early as 1884, Marshall McDonald developed a theory that shad are restricted to a narrow range of temperatures and that the timing of shad runs thus depends on when the water warms. McDonald (1884, p. 599, 604, 605) stated that shad

> ... occupy an hydro-isothermal belt, or area, limited by the temperature of 60° F. to 70° F.; that they move with this belt, *i.e.*, as the season advances, into and up the rivers....
>
> ... In the Savannah River they appear early in January, and in the Neuse River at a period not much later than in the Savannah. In the Albemarle the important Shad seine-fisheries begin early in March, but doubtless the fish are in the Sound some time before that date; not, however, in numbers sufficient to justify the great expenses attendant upon the operation of these large seines. In the Chesapeake Bay they make their appearance in February, although the height of the fishing season in its waters is during April and May, and at a date somewhat later in the more northern tributaries. In the Delaware, Connecticut, Merrimac, and St. John (Nova Scotia) Rivers, Shad are first seen at periods successively later as we proceed farther north. The date of their first appearance in any of these waters, however, varies from season to season, the limit of such variation being from three to four weeks.
>
> These irregularities in the time of the run into our rivers, which cause so much perplexity and discouragement to the fishermen, are, however, readily explained when we keep in view what has been already said in regard to the influences of temperature in determining the movements of these fishes.

McDonald pointed out that the shad run in a particular river may be delayed if the water cools. Although rising temperatures accelerate the run, a sudden increase may also retard it. The downstream migration of the juvenile shad occurs when water temperatures fall to below 60°F (15.5°C).[3] In support of his thesis, McDonald provided a table of daily shad catches and water temperatures in the Potomac River for the year 1881. Shad were caught in water from 8.0° to 24.5°C. We performed a frequency analysis of these data which shows that the average shad was associated with a temperature of 18.5°C. Ninety percent of the run took place between 12.0° and 21.0°C. McDonald also supplied a table showing monthly average water temperatures for the St. Johns River, Fla., in 1877 and 1878. He stated that shad first appeared in November when the average temperature was 63.5°F (17.5°C) and that spawning took place in February and March when the average temperatures were 58.0° and 62.2°F (14.5° and 17.0°C). McDonald provided no quantitative data on shad in the St. Johns River, however, and his thesis therefore apparently rests on data from the one year and one river in which both shad catches and water temperatures were available. He gave no data to support his statement on migrations of juveniles.

Working in the field, one readily becomes convinced as did McDonald (1884) that water temperature affects the run of shad. This observation has also been made by Leim (1924), Talbot (1954), and Massmann and Pacheco (1957). The difficulty has been to develop a quantitative measure or prediction of the effect. Talbot (1953), by means of linear regression, analyzed the timing of the shad run in relation to river flow and river temperature at Bonneville Dam on the Columbia River. Temperatures and flows are recorded there, and Talbot had available shad counts made from 1938 to 1950 as the fish ascended the fish ladders at the dam. He concluded that flow and temperature do affect the time of entry of shad into the river, although the correlation coefficient of time of the run and temperature was not quite significant at the 5% level.

Now 19 more years of data are available (Table 1). The 32 years of data show a highly significant partial correlation of temperature, as well as a significant partial correlation of flow, with the timing of the shad run. Of course, this

[3] All temperatures used in developing this paper were originally recorded in Fahrenheit. Our conversions to Celsius have been rounded to the nearest 0.5°C.

TABLE 1.—Time of median shad passage at Bonneville compared with time when temperature exceeded 15.5°C and flow diminished to 325,000 cfs and number of days counted from May 31 (shown in parentheses).[1]

Year	Date on which: Half of shad were counted		Temperature rose above 15.5°C		Flow decreased to 325,000 cfs	
1938	July 24	(54)	June 24	(24)	July 17	(47)
1939	July 7	(37)	June 26	(26)	June 12	(12)
1940	June 30	(30)	June 9	(9)	June 16	(16)
1941	July 5	(35)	June 5	(5)	May 30	(—1)
1942	July 21	(51)	June 28	(28)	July 1	(31)
1943	July 20	(50)	June 29	(29)	July 24	(54)
1944	July 17	(47)	June 21	(21)	June 21	(21)
1945	July 13	(43)	June 18	(18)	July 4	(34)
1946	July 8	(38)	June 29	(29)	July 13	(43)
1947	July 4	(34)	June 16	(16)	July 4	(34)
1948	July 18	(48)	July 19	(49)	July 13	(43)
1949	July 11	(41)	July 13	(43)	June 22	(22)
1950	July 21	(51)	July 7	(37)	July 28	(58)
1951	July 8	(38)	June 16	(16)	July 25	(55)
1952	July 15	(45)	June 21	(21)	July 8	(38)
1953	July 15	(45)	June 30	(30)	July 20	(50)
1954	July 25	(55)	July 7	(37)	July 30	(60)
1955	July 23	(53)	July 12	(42)	July 29	(59)
1956	July 14	(44)	June 29	(29)	July 15	(45)
1957	July 11	(41)	June 20	(20)	July 25	(55)
1958	July 7	(37)	May 30	(—1)	July 28	(58)
1959	July 17	(47)	June 22	(22)	July 18	(48)
1960	July 5	(35)	June 4	(4)	July 12	(42)
1961	July 7	(37)	June 16	(16)	July 4	(34)
1962	July 13	(43)	June 15	(15)	July 29	(59)
1963	July 8	(38)	June 13	(13)	July 1	(31)
1964	July 14	(44)	June 29	(29)	July 24	(54)
1965	July 1	(31)	June 23	(23)	July 14	(44)
1966	July 8	(38)	July 16	(46)	July 19	(49)
1967	July 12	(42)	June 21	(21)	July 17	(47)
1968	July 3	(33)	June 12	(12)	July 1	(31)
1969	June 21	(21)	June 3	(3)	June 19	(19)

Shad-temperature partial correlation $r = 0.58$, $P<0.01$
Shad-flow partial correlation $r = 0.44$, $P<0.05$
Temperature-flow partial correlation $r = -0.004$ not sig., df = 29

[1] Method is that of Talbot (1953) as are data 1938-1950, data 1951-1969 from Corps of Engineers (1951-1969).

analysis suffers from the usual defects of data on two or more factors which may trend in the same direction without necessarily being related in a cause-and-effect manner. For example, we do not believe that the significant correlation of flow and the timing of the runs has any particular meaning beyond the fact that the shad run occurs after flows begin to decline. Shad migrate into streams of various sizes, and we do not think that they select a particular flow in a particular stream. On the other hand, the fact that they select the same water temperature in different streams and, as will be shown later, that in their oceanic migration they remain in water of the same temperature points to the conclusion that the timing of the shad run is related to water temperature.

To find the particular temperature preferred by shad, we tabulated the temperature when each fish was counted at the Bonneville fish ladders. For each year we then calculated an average of these temperatures. This amounts to determining the temperature at the peak of the shad run (Table 2). Such a procedure is justified by the large samples and the fact that the frequency distribution is approximately normal. Very little variation in the temperature at the peak of the run occurred from year to year. Most of the time the peak occurred at 18.0°C. In 78% of the years the peak appeared in the range 16.5° to 19.0°C. (Table 3). In the average year, 90% of the shad run was counted when the temperatures ranged between 15.5° and 19.5°C. In 26 of the 32 years the temperature varied only 4.0°C or less during the time when 90%

TABLE 2.—Water temperatures (°C) associated with the peak of the shad run and lower and upper temperatures associated with the middle 90% of the shad counted at Bonneville Dam fishways,[1] Columbia River.

Year	Lower	Peak	Upper	Difference
1938	17.0	19.5	21.5	4.5
1939	15.0	17.0	21.0	6.0
1940	17.0	19.0	20.0	3.0
1941	17.0	20.0	23.0	6.0
1942	17.0	19.5	21.0	4.0
1943	16.0	18.0	19.0	3.0
1944	17.0	14.0	21.0	4.0
1945	18.0	19.5	20.5	2.5
1946	15.0	16.5	19.0	4.0
1947	16.0	18.0	19.5	3.5
1948	17.0	19.5	20.5	3.5
1949	13.5	15.5	16.5	3.0
1950	16.5	18.0	19.0	2.5
1951	15.5	17.0	19.0	3.5
1952	15.5	18.5	19.5	4.0
1953	16.5	18.5	19.0	2.5
1954	15.0	16.5	18.0	3.0
1955	14.5	17.0	19.0	4.5
1956	16.0	18.5	20.0	4.0
1957	15.5	18.5	20.0	4.5
1958	18.5	20.0	22.0	3.5
1959	16.5	18.5	20.0	3.5
1960	15.0	18.0	20.0	5.0
1961	16.5	18.5	20.5	4.0
1962	16.5	18.0	20.0	3.5
1963	16.0	18.0	19.0	3.0
1964	15.5	18.0	19.0	3.5
1965	16.0	18.0	19.5	3.5
1966	15.0	16.5	19.0	4.0
1967	17.0	18.5	19.5	2.5
1968	15.5	16.5	19.0	3.5
1969	16.0	18.0	19.0	3.0
Mean	16.0	18.0	19.5	3.5

[1] From Corps of Engineers (1948-1969) and unpublished data for which we are indebted to Ivan Donaldson, Corps of Engineers, and Kingsley G. Weber, National Marine Fisheries Service.

TABLE 3.—Number of years when given temperature was recorded at the peak of the spawning run.

Temperature at peak (°C)	Number of years	Percentage of years
15.5	1	3
16.0	0	
16.5	4	
17.0	3	
18.0	9	78
18.5	7	
19.0	2	
19.5	4	19
20.0	2	

TABLE 4.—Water temperatures (°C) associated with the peak of the shad run and lower and upper temperatures associated with the middle 90% of the shad counted at Holyoke Water Power Company fishway, Connecticut River.

Year	Lower	Peak	Upper	Difference
1955	19.0	19.5	23.5	4.5
1956	19.0	21.0	23.0	4.0
1957	18.5	19.5	22.5	4.0
1958	16.0	18.5	18.5	2.5
1959	17.0	20.5	23.0	6.0
1960	15.5	19.5	20.0	4.5
1961	15.0	18.5	21.5	6.5
1962	16.0	20.5	21.0	5.0
1963	16.5	20.0	21.5	5.0
1964	16.0	19.5	20.5	4.5
1965	16.5	19.0	21.5	5.0
1966	17.0	19.5	21.0	4.0
1967	16.5	20.0	23.0	6.5
1968	14.5	17.0	21.5	7.0
1969	16.5	19.0	22.0	5.5
Mean	16.5	19.5	21.5	5.0

of the shad appeared at the Bonneville fish ladders. In only 3 years did the range exceed 4.5°C (Table 2).

The only comparable data that we have been able to locate on the Atlantic coast concern the shad passed by the fish lift of the Holyoke Water Power Company located 138 km from the mouth of the Connecticut River. Daily records of water temperature and the number of fish lifted over the dam show that few shad were passed when the water temperature was below 14.0°C. Peak passage occurred at temperatures ranging from 16.5° to 21.5°C (Table 4). This compares closely with the temperature of peak shad passage (16.5°-19.0°C) at Bonneville Dam, 233 km from the mouth of the Columbia River.

Commercial catches provide less direct, and therefore less reliable, data on the timing of shad runs. These can be affected by many extraneous factors such as market price, which leads to heavier sampling in the early part of the run, and turbidity of the water, which would have the same effect because catch per effort would be higher early when turbidity is high. Nevertheless, the temperatures found to be associated with peak commercial catches are in general agreement with those associated with actual counts at the fishways.

For the St. Johns River, Fla., mean weekly shad catches (in pounds) were calculated from daily catch records of the Morris Crab Company for the years 1962 to 1967. These are plotted in Figure 1 with mean monthly river temperatures developed from daily temperature records of the Florida Light and Power Company for the years 1960 to 1967. Fishing effort was approximately equal from day to day and year to year from mid-November to mid-March, but after this time market fluctuations resulted in sporadic fishing effort. In order to eliminate error resulting from sporadic fishing effort, catches made after mid-March were omitted from the analysis.

Shad migrations in the St. Johns River corresponded closely to the period of lowest annual river temperatures, confirming the earlier observations of McDonald (1884). Few, if any, shad entered the river at temperatures in excess of 20.0°C prior to mid-November, and peak numbers occurred in mid-January when temperatures were at the annual low (15.0°C). As temperatures increased, in February and March, the relative abundance of shad declined.

Massmann and Pacheco (1957) investigated the relationship between temperature and shad catch in the York River, Va., in the years 1953 to 1956. From their data we calculated the mean catch of shad per net day, by weekly intervals, February 15 to June 1. The relationship between the timing of shad migrations in the York River and mean monthly river temperatures (developed from daily records for the period 1953 to 1962 that were supplied by the Virginia Institute of Marine Science) is illustrated in Fig-

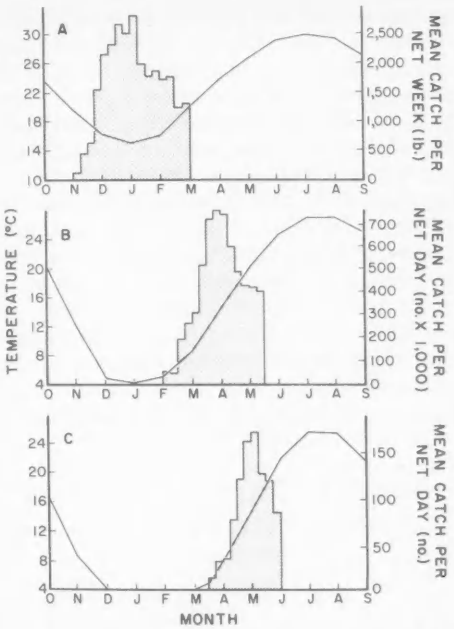

FIGURE 1.—Shad catches at various temperatures in three Atlantic coast rivers. (A) St. Johns River, Fla.—temperatures are averages, 1960-1967; shad catches in pounds are from weekly catches of the Morris Crab Company, 1962-1967. (B) York River, Va.—temperatures are averages, 1953-1962; shad catches are numbers per net day, 1953-1956 (Massmann and Pacheco, 1957). (C) Connecticut River, Conn.—temperatures are averages, 1958-1969; shad catches are numbers per net day, 1944-1964 (courtesy Angelo Baldi) and 1965-1969 (Leggett, 1969).

ure 1. Few, if any, shad entered the York River until late January when river temperatures exceeded 4.0°C, and peak numbers were captured in April at temperatures around 14°C. At higher temperatures catches declined.

For the Connecticut River the mean catch of shad per net day, by weekly intervals, April 1 to June 15, was estimated from the daily catch records of commercial fisherman Angelo Baldi for the period 1944 to 1964, and from the daily records of shad captured for tagging by biologists of the Essex Marine Laboratory from 1965 to 1969. These data are presented in Figure 1, together with mean weekly river temperatures developed from daily water temperature records of the Hartford Electric Light Company, and Essex Marine Laboratory for the period 1958 to 1969. Shad are generally soft-bodied and of little economic value after mid-June; from then on fishing effort is much reduced and is more sporadic. For this reason, the histogram of mean weekly catch was terminated in mid-June. Shad first entered the Connecticut River from late March to early April when water temperatures ranged from 4.0° to 6.0°C. The mean weekly catch increased with temperature until mid-May when temperatures averaged about 15°C. Catches declined steadily at higher temperatures. During the period for which accurate daily temperature records were available, 1958 to 1969, the mean temperature at which the peak catch was obtained at the mouth of the river was 13.0°C (Table 5). In 10 out of 12 of those years, the peak catch occurred at temperatures between 11.0° and 15.5°C. In the Connecticut River, a large sport fishery for shad operates at Enfield, in the area 88 to 109 km from the river mouth. A daily record of the number of anglers and the number of shad caught in a State-controlled fishing area has been maintained since 1942. A daily record of the water temperature at the fishing area has also been kept. Most shad were caught by angling at temperatures ranging from 11° to 18°C (Table 6). On the average, the peak occurred near 15°C. As noted previously, the temperature of peak shad passage at Holyoke, 29 km farther upriver, occurred at temperatures averaging 19.5°C and ranging from 16.5° to 21.5°C.

TABLE 5.—Water temperature (°C) associated with peak of shad catch and upper and lower temperatures associated with middle 90% of the catch at Saybrook, Conn.

Year	Lower	Peak	Upper	Difference
1958	8.5	11.5	19.0	10.5
1959	6.0	13.5	22.0	16.0
1960	10.0	15.5	20.0	10.0
1961	10.5	13.5	16.5	6.0
1962	12.5	14.5	22.0	9.0
1963	10.0	14.5	20.5	10.5
1964	8.0	13.5	18.5	10.5
1965	8.5	14.0	20.0	11.5
1966	8.5	9.5	13.0	4.5
1967	6.5	9.5	13.5	7.0
1968	12.0	13.0	16.5	4.5
1969	8.5	11.0	14.5	6.0
Mean	9.0	13.0	18.0	9.5

TABLE 6.—Water temperatures (°C) associated with the peak of the shad run and lower and upper temperatures associated with the middle 90% of the shad caught by anglers at Enfield, Conn.

Year	Lower	Peak	Upper	Difference
1953	8.0	12.0	16.5	8.5
1954	8.0	10.5	14.0	6.0
1955	15.5	18.0	18.0	2.5
1956	11.0	14.5	18.0	7.0
1957	14.0	16.0	18.0	4.0
1958	11.0	16.0	17.5	6.5
1959	14.0	18.5	18.5	4.5
1960	14.0	16.0	20.5	6.5
1961	9.0	14.0	16.5	7.5
1962	8.5	16.0	21.0	12.5
1963	12.0	16.5	16.5	4.5
1964	11.5	17.0	18.5	7.0
1965	11.5	17.0	23.0	11.5
1966	9.0	15.0	18.5	9.5
1967	8.0	13.5	20.0	12.0
1968	11.0	15.0	15.5	4.5
1969	11.5	14.5	18.5	7.0
Mean	11.0	15.5	18.0	7.0

TABLE 7.—Water temperatures and counts per hour of downstream migrating juvenile shad at Matamoras, Pa., September and October 1951. (From Sykes and Lehman, 1957.)

Date		Temperature °C	Shad per hour
September	10	20.5	5
	17	20.5	0
	21	20.5	1
	24	21.0	0
	28	20.0	10
	29	18.0	20
	30	14.0	65
October	1	17.0	59
	5	21.0	0
	8	14.0	600
	9	14.0	600
	10	15.0	300
	13	15.0	350
	14	14.0	350
	15	14.0	70
	16	14.0	10
	17	15.5	0
	19	15.0	0
	29	15.0	0

As these data clearly show, the timing of shad spawning migrations is highly correlated with specific water temperatures in all three of the rivers studied. Most shad entered these rivers when temperatures were between 10.0° and 15.0°C, even though this required considerable variation in the timing of shad to changing temperature conditions in the three rivers. In the St. Johns River (Fla.), water temperatures seldom fall below 14.0°C, and the spawning run occurs at about the seasonal temperature minimum in January. These Florida shad must begin to enter the river during conditions of declining water temperatures, as opposed to the shad from the York and Connecticut Rivers which begin their migrations as temperatures are increasing above an apparent lower limit of 4.0°C. In Florida, most of the migration occurs while river temperatures are below 20.0°C. Maximum movements of shad into the York and Connecticut Rivers occur at temperatures of about 15.0°C. The sporadic nature of fishing effort late in the runs when temperatures were higher probably leads to an underestimate of temperatures, but in all three rivers the mean weekly catch at 19.0° to 21°C was approximately one-half that recorded at 13.0° to 15.0°C.

TIMING OF OUTMIGRATION OF JUVENILES RELATED TO STREAM TEMPERATURE

Juvenile shad normally spend their first summer in the river in which they were spawned. They begin to move downstream to the sea in the fall. This migration, too, is apparently triggered by temperature. Sykes and Lehman (1957) provided the interesting quantitative data in Table 7. The largest number of shad moved downstream when the temperature dropped below 15.5°C for a period of several days. Similar findings were reported by Smith (1899), Walburg and Nichols (1967), and Chittenden (1969).

OCEANIC WATER TEMPERATURES ASSOCIATED WITH SHAD MIGRATIONS

Talbot and Sykes (1958) were the first to describe the oceanic migrations of shad. From 19 years of tagging by the U.S. Fish and Wildlife Service, they learned that shad from all the major Atlantic coast rivers congregate in the Gulf of Maine in the summer and fall. This group of shad includes immature fish from all streams and survivors of spawning from streams north of Chesapeake Bay. South of Chesapeake Bay there are no survivors after spawning. Talbot

and Sykes believed that the shad move south to waters off the Middle Atlantic States in the winter. However, they had only one recapture in December. In January or February shad do begin to appear off the central Atlantic Coast from North Carolina to Long Island. Confirmation of the conclusions of Talbot and Sykes (1958) came from Walburg and Nichols (1967) who reported 49 shad caught at lat 40°N, long 70°41'W (Point A, Figure 2A), January 23 to February 2, 1961, by the research vessel *Delaware*. If mature in the spring, the shad then move either north or south to their home streams and spawn. The shad runs in southern streams occur early in the spring and progressively later northward.

One of us (Leggett) has conducted extensive tagging studies of Connecticut River shad since 1965. From 1965 to 1969, 18,374 mature shad were marked and released in the lower Connecticut River. In all, 83 of these shad have been recovered along the Atlantic coast from North Carolina to the Bay of Fundy, 66 with complete information as to date and place of recapture. Over 300 shad were recovered in the lower Connecticut River 1 year or more after tagging. These recaptures, together with coastal recoveries from 4,500 shad tagged by the U.S. Bureau of Fisheries and U.S. Fish and Wildlife Service between 1938 and 1949, were plotted on monthly surface temperature charts of the western Atlantic Ocean (U.S. Naval Oceanographic Office, 1967; U.S. Coast Guard Oceanographic Unit,

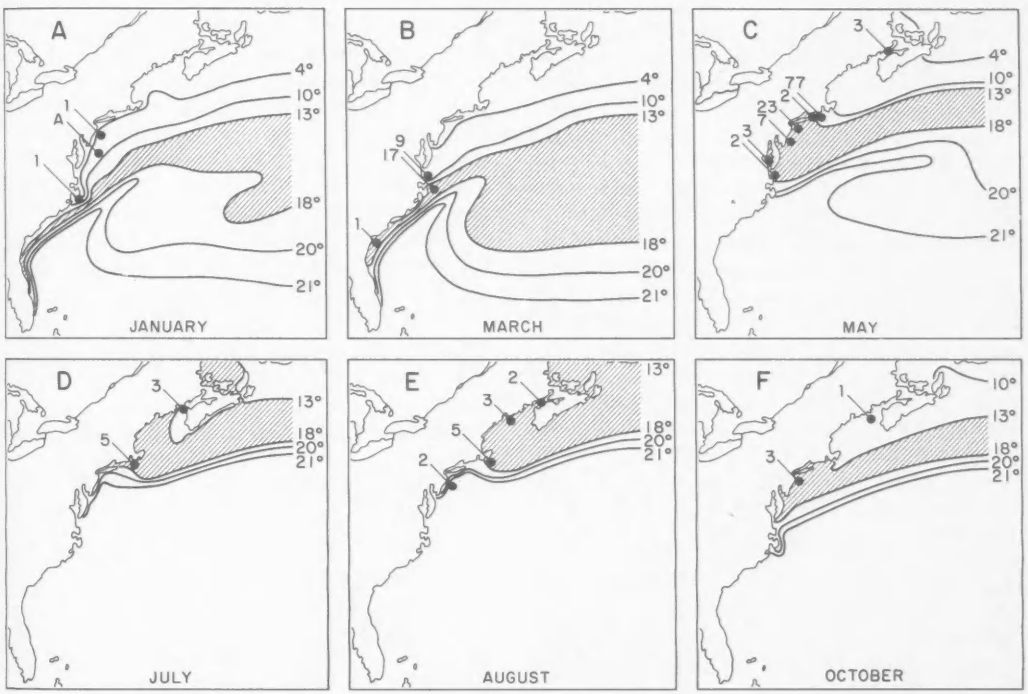

FIGURE 2.—Atlantic Ocean average sea surface temperatures and associated locations of shad recaptures for selected months. Number of recaptures is shown. Point A represents the 49 shad Walburg and Nichols (1967) reported caught in a trawl. (Temperature charts adapted from U.S. Naval Oceanographic Office, 1967; inshore segments of isotherms were refined with the aid of surface temperature charts by U.S. Coast Guard Oceanographic Unit, 1969-1971, see footnote 4.)

1969-1971).[4] Their distribution in time and space corresponds closely to the position of the 13° to 18°C isotherms. Six of these charts are presented in Figure 2.

In July, August, and September, the 13° to 18°C isotherms are situated in the Gulf of Maine (Cape Cod to Bay of Fundy). It was from here that Talbot and Sykes (1958) reported the majority of their recoveries in these months. Recoveries from the Connecticut River taggings were confined exclusively to this area during July (Figure 2D), August (Figure 2E), and September. In October (Figure 2F), November, and December these waters cool and the 13° to 18°C isotherms move south to the middle Atlantic region, the general area where shad are said to winter (Talbot and Sykes, 1958; Walburg and Nichols, 1967). During these months, as stream temperatures drop below 15.5°C, juvenile shad migrate out of their streams and, as Talbot and Sykes suggested, they probably join the large body of southward migrating adult and immature shad as they pass on their way to the middle Atlantic wintering area.

In December and January (Figure 2A), water of appropriate temperature extends in a narrow band near the coast of Florida, and the shad can move into the St. Johns River along the band. In February and March (Figure 2B), 13° to 18°C water bathes the coast of the southern Atlantic States from Cape Hatteras south providing access for shad to coastal streams in those States. At this time Connecticut River shad first appear off the coast of North Carolina and Virginia and begin to move north along the coast, mainly within the bounds of the 13° to 18°C isotherms. During April and May (Figure 2C), shad continue to move north as they follow the movement of the 13° to 18°C isotherms. In April they are located around Chesapeake Bay and Delaware Bay and contribute to the runs into streams in these areas. By May shad are concentrated in the Long Island region and run into the Hudson and Connecticut Rivers. In June there is movement of the isotherms farther north along the coast, corresponding to the peaks of the shad runs in streams to the north. Again in July (Figure 2D), August (Figure 2E), and September, the Gulf of Maine reaches optimum temperature for the species.

The northern and southern limits of the range of shad on the Atlantic coast appear to be defined by the temperature relationship described above. In June and July a narrow tongue of 13°C water typically extends to the mouth of the St. Lawrence River, the northern extension of the fish's range. North of the St. Lawrence, the ocean seldom warms above 13°C. In the south shad appear to be blocked from extending their range into the Gulf of Mexico by a band of water south of Cape Kennedy that rarely cools below 21°C even in December and January (U.S. Naval Oceanographic Office, 1967). It is probable that *Alosa alabamae*, a closely related species that is native to most principal streams tributary to the Gulf of Mexico east of the Mississippi, evolved from *Alosa sapidissima*. Prior to the emergence of the Florida peninsula, the range of shad may have included these Gulf rivers. Florida's emergence would have produced an effective geological barrier between the stocks, thereby promoting their separate evolution. In this connection we note that a narrow band of water of the temperature range 13° to 18°C extends along the northernmost coast of the Gulf of Mexico during the months of December to March (Rivas, 1968).

PACIFIC OCEAN MIGRATION OF SHAD

Prior to 1871 shad occurred only on the eastern coast of North America. In that year shad from eastern rivers were stocked in the Sacramento River. So successful was the venture that by 1880 shad were reported to range from Todos Santos Bay, Baja California, to Kodiak, Alaska (Welander, 1940; Claussen, 1959). Shad make no spawning runs south of San Francisco Bay because there are no streams of sufficient size. The Fraser River is thought to be the most northerly river in which they spawn (Carl, Clemens, and Lindsey, 1967).

Nothing concrete is known about the migrations of the shad in the Pacific Ocean but cir-

[4] U.S. Coast Guard Oceanographic Unit. 1969-1971. Monthly temperature charts, July 1969 to December 1971, available U.S. Coast Guard Oceanographic Unit, Airborne Radiation Thermometer Program, Bldg. 159-E Washington Navy Yard, Washington, D.C. 20390. [Processed.]

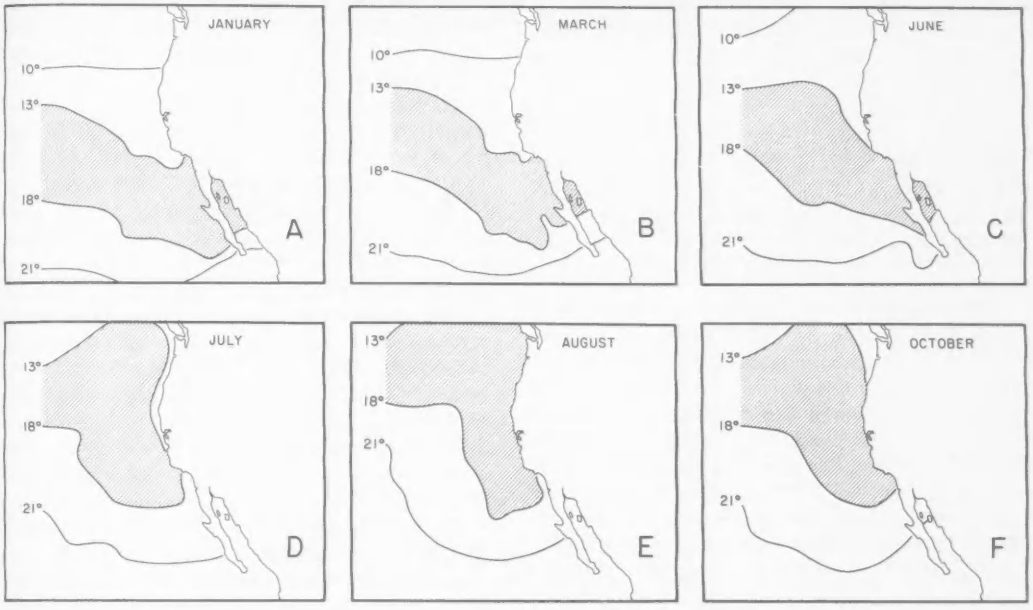

FIGURE 3.—Pacific Ocean average sea-surface temperatures and predicted shad distributions for selected months. (Temperature charts adapted from U.S. Navy Hydrographic Office, 1954.)

cumstantial evidence suggests a northward migration in summer and a southward one in winter as on the Atlantic coast.

If we assume that the migrations of shad in the Pacific follow the same specific ocean temperatures as do the migrations of Atlantic coast populations (an assumption that is supported by the similar relationships between peak movements into rivers and water temperatures on the two coasts), it is possible to make predictions concerning the Pacific migrations based on our knowledge of the distribution of 13° to 18°C waters along the Pacific coast.

During the months of December to April, the 13° to 18°C isotherms encompass an area extending from southern California to near the tip of Baja California (Figures 3A, 3B). We predict that the Pacific shad populations will be found to winter in this general area, a prediction strengthened by records of a few shad from San Pedro, Calif., in November and December (Smith, 1896). In May and June a general warming trend is noticeable along the coast, and the 13° to 18°C isotherms arch northward offshore (Figure 3C). Their northward movement is undoubtedly affected by the upwelling that occurs along the California and Oregon coasts and produces an inshore pool of cool water in spring and summer. We predict that the shad begin their northward movements at this time. If this be so, they are probably directed offshore in the area of this cool water. In July and August, 13° to 18°C waters occur over a wide range of the Pacific Ocean (Figures 3D, 3E). Shad might be located anywhere from Alaska (in some years) to Baja California. The reports, summarized by Welander (1940), of rare summer occurrences of shad at Kodiak, Alaska, and by Claussen (1959), off Baja California, are therefore not surprising. In September, cooling commences and results in a southward movement of suitable water and a contraction of its extent (Figure 3F). During this period we predict that the shad move southward with the 13°

to 18°C isotherms, resulting in their concentration off southern California and Baja California in late November and December and continuing at least until April.

The scope of regular migrations that we hypothesize as taking place on the Pacific coast (about 2,575 km, Columbia River to Cedros Island) is similar to that which is known to occur on the Atlantic coast (about 2,250 km, St. Johns River, Fla., to the Bay of Fundy).

DISCUSSION

Both the marine and freshwater migrations of shad appear to be regulated by water temperature. In the four rivers we have considered, the temperatures at which shad appeared in the river and at which peak movement occurred were remarkably consistent in spite of the great distances separating them. In all rivers except the St. Johns in Florida, water temperatures are increasing as the shad proceed upriver. Water temperature in this river is decreasing during the first half of the run, and the peak movement occurs at the lowest annual temperature. Nevertheless, the peak occurred in the same temperature range (15.5°-20.0°C) in the St. Johns as in the other rivers studied.

The precise correlation between temperature and the timing of the spawning migrations of the shad places the maximum number of adults on the spawning grounds when the temperature is optimum for the survival of eggs and young. In the Columbia and Connecticut Rivers, where our studies of shad movement were conducted at points close to the spawning grounds (Bonneville and Holyoke), peak migrations occurred at 18.0° and 19.5°C, respectively. Massmann (1952) working in the York River, Walburg (1960) in the St. Johns River, and Marcy (1969) in the Connecticut River have all reported the median spawning temperature, as shown by abundance of eggs, to be within the temperature range of 16° to 20°C. Leim (1924) and Bradford, Miller, and Buss (1964)[5] found that maximum hatch and survival of eggs and larvae occurred at 15.5° to 26.5°C. Temperatures below 15.5°C prolonged the time of hatching and reduced survival.

Since these optimum temperatures are reached later in the year at higher latitudes, the timing of the entry of shad into individual rivers must also be seasonally adjusted. Consequently, the earliest run occurs in Florida during the winter, and the latest runs in June and July in northern rivers such as the St. Lawrence and Columbia. This phase of the timing appears to be regulated by the adherence of shad to similar temperature regimes while at sea. As the ocean warms in the spring, the area occupied by water temperatures in the range 13° to 18°C moves gradually northward. By maintaining themselves in this thermal zone, shad arrive at the mouth of their home river when river temperatures are suitable for entry.

Of course, what we have described is a general migratory pattern of shad that is clearly associated with water temperatures both in the ocean and in the streams into which they run. Occasional shad are caught in the winter in Chesapeake Bay and in the Delaware and Hudson Rivers in the fall and winter (summarized by Walburg and Nichols, 1967, also recorded in our recoveries of Connecticut River shad shown in Figures 2A, 2F.) We learned recently that 14 shad were caught in a commercial trawl on February 10, 1972 at lat 41°16′N, long 71°39′W where the water temperature was 3.7°C at the surface and 4.1°C at the bottom. Nevertheless, as Walburg and Nichols stated: "The vast majority of fish, however, followed a regular migratory pattern." It may very well be that the observed temperatures associated with the presence of the majority of shad are preferred temperatures, not required ones, or they may be required only by a majority of fish. A small minority may be able to condition themselves to water outside the range tolerated by the majority. Experiments are needed to determine the upper and lower units of temperature tolerance of mature and immature shad, as well as their temperature preference.

It should be noted that we have related average ocean conditions to an average shad migra-

[5] Bradford, A. D., J. G. Miller, and K. Buss. 1964. Progress report summary on phase B-2 "to determine by bioassay techniques the inherent tolerance of shad during its egg and larval stages to specific environmental factors of the Susquehanna River and its tributaries. Pennsylvania Fish Commission, Benner Spring Fish Research Station, Bellefonte, Pa. (Unpubl. manuscr.)

tion. In particular years the ocean temperature regime may vary and change the usual locations of the shad. Moreover, we have related shad migrations to surface temperatures only. There is at present no information on the depths at which shad migrate. Walburg and Nichols (1967) recorded shad that were trawled at depths of 87 to 126 fm, and Leggett has similar records of recoveries of tagged shad at depths of 20 to 70 fm, again by trawl. These records do no more than provide estimates of the maximum depths at which shad migrate. These fish may have been captured near the surface as the trawl was being recovered.

On the basis of our observations on the behavior of shad in relation to temperature, we believe that the effect of a significant elevation of the temperature of a northern stream might be to initiate the shad run at an earlier date, provided that ocean temperatures are within the proper range. In a southern stream like the St. Johns River, Fla., where the run occurs during the natural cooling phase rather than the warming phase of the river, elevated temperatures could destroy the run of shad.

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AN EXPOSITION ON THE DEFINITION OF FISHING EFFORT[1]

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ABSTRACT

The term "fishing effort" is well defined in population dynamics literature. The term as defined in the population dynamics literature is, however, difficult to reconcile with broader definitions of fishing effort, particularly those having economic implications. The present paper discusses the distinction between the definitions and gives some examples in the context of allocating inputs, the capacities of fishing boats, and several stocks to the catch in a manner which maximizes profits. Managerial behavior is also an important input to the fishing process; this is discussed in a decision theory format where decision quality can be measured relative to entropy in the decision environment affording a comparison among decision environments in terms of information and an imputed valuation of a bit of information under various circumstances. The conventional measures of the quality of the decision environment are often based upon expected catch. Alternate measures are discussed which include the expected loss or the risk involved in the decision process.

The deployment of fishing effort is one of the fundamental components of fishery management. While fishing effort has been rather precisely defined in the population dynamics literature, effort has not been well defined in its broadest context. This paper considers the definition of fishing effort with special reference to the development of techniques which are useful not only for the definition of effort in the usual strategic sense, but for the definition of effort in the tactical and operational sense as well. This definition is requisite for considering fishing as a total system (see Rothschild, 1971).

The transformation of wild stocks of fish into the "catch" is generally considered to be mediated by the quantity of fishing effort expended in the process of harvesting the catch. The measurement of the magnitude of fishing effort is of central importance to the theory of the dynamics of exploited fish populations because the various "optimal" catches which are developed in this theory must ultimately be related to optimal quantities of fishing effort. On one hand it seems quite obvious that fishing effort should be related to quantities that can be thought of as "inputs" to the fishing process, quantities such as hours fished, fuel consumed, number of fishermen, etc. Therefore, it is at least to some extent somewhat paradoxical that the basic definition of fishing effort which is used in population dynamics, and commonly used in most fishery management applications, does not necessarily refer to any of these usual "inputs." Fishing effort is defined in terms of the catch; that is, one unit of real or nonnominal effort is simply the numerical fraction of the average population that is caught. In order to emphasize this point, consider two fishing fleets. Each fleet fishes on separate populations which are in every respect identical. The fleets make identical catches and, therefore, each removes identical fractions of the average populations from each population. By definition, then, these two fleets both exert the same amount of fishing effort. The fact that "inputs" are not implicit in the theory can be seen by identifying the first fleet as consisting of 100 modern trawlers and the second as, perhaps, 10 pleasure yachts that have been modified just enough to enable them to catch fish. Even though both fleets exert equivalent amounts of fishing effort, their inputs—indexed by, say,

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the costs of their operations—must differ considerably. This, of course, in no way invalidates the population dynamics theory and there are, in fact, methods for converting fishing effort, defined in terms of the magnitude of the catch, into numbers of fishing boats, etc. There is an extensive literature on this subject and, because of this, there is no need to prolong the discussion of this particular aspect of the fishing-effort problem. Rather, we shall concentrate on aspects of the problem of identifying and measuring inputs to the fishing process as well as discussing the methodology of relating the set of inputs to the outputs (the catch), which can, as we will see by the ensuing discussion, be treated in terms of several species and even, if necessary, in terms of strata (such as, for example, size classes) within several species. These aspects of the problem simply relate to the theory of production functions. Production functions have seldom been treated in fisheries, but when they have, they have been approached primarily from a regression analysis point of view. It is not clear, even given that we meet the assumptions of the estimation procedures and thus obtain credible statements on the "good properties" of the estimation procedure, that the curve fitting technique can do much more than describe, in an artificial way, the status quo; there is no inherently good advice in the curve fitting procedure on optimality; optimality must be implicitly assumed. What is needed are techniques of finding those combinations of inputs that produce extrema in the outputs, as well as to determine the sensitivity of this input-output system to changes in the magnitude of the inputs, and a reevaluation of the input-output system which will acknowledge the stochastic aspects of the decision process.

Our analysis of the fishing effort problem is divided into several parts. First, the fishing-effort problem is recast as a production function problem whereby valuable inputs to the fishing process are allocated among the outputs of the process in a manner which maximizes profit. In the particular example chosen the inputs are the capacities of three sizes of fishing boats in a fleet and the "catchable stocks" of two species of fish, yellowfin and skipjack tuna, whereas the outputs are the catches of the various species in the different boats. The components of the yellowfin and skipjack tuna catchable stocks are allocated among the various size vessels in the fleet to maximize profits. The technique used to explore the maximization of profits is linear programming. The technique enables the simultaneous exploration of fleet technological constraints, the interaction of multiple species as inputs to the decision process, and the range within which catches can be set without changing the nature of the profit maximization equation. Easy algebraic extensions of the model can be seen to have rather important implications. For example, instead of allocating two species of fish among three boat classes, the stocks of i species can be allocated among j classes of boats and k fishing nations. The ease of such an extension may, however, be somewhat deluding, particularly because of the difficulty in defining appropriate coefficients and constraints respecting the allocation among the k nations. Nevertheless the difficulty does not preclude solution and furthermore placing the problem in this context enables a much needed formulation of the problem of allocation of fish stocks among countries.

Most input-output analyses involve physical inputs and outputs. This was true in the example cited above. A classic example in fisheries is that of fishing power which is frequently related to fishing vessel horsepower. There are many instances, however, where the physical inputs (horsepower, fleet capacity, etc.) are less important than those related to the skill utilized by the fisherman in making managerial decisions such as where to fish, when to fish, when to stop fishing, etc. So, in the second part of this paper we consider the development of a decision theory model for adjudging fisherman skill in a "real world" probabilistic environment and show how the quality of the fisherman's skill in decision making relates to the entropy of his decision environment. Many important applications of this theory beyond the examples utilized in the text, such as the decision of whether to fish species a or species b when both species are available or whether to fish on one ground such as the eastern tropical Pacific tuna grounds or to move to an-

other ground such as the tuna grounds off the west coast of Africa.

The third part of the paper considers, given the possibility that inputs and outputs can be related and that decision skill can be judged, that different fishermen apply different criteria to the signals that they obtain from their decision environment. This question is discussed in terms of maximizing catch versus minimizing risk in attaining the catch. One of the main conclusions that can be derived from the following discussion is that advances toward the management of fisheries as a total system which considers the strategic, tactical, and operational hierarchies and the flow of information and material among these are not limited by analytic techniques. The limitation arises from a lack of explicit formulation of the kinds of data needed for the development of a total management system.

INPUT-OUTPUT ANALYSIS

Let us contrive a simple production function problem in a linear-programming context. This approach is treated in some detail by Dorfman, Samuelson, and Solow (1958). We should mention that the linear-programming technique is, of course, not without assumptions, and these are discussed in any operations research text (for another application of linear programming in salmon management see Rothschild and Balsiger, 1971). Violations of the assumptions required for the linear-programming model are usually handled by other techniques in mathematical programming theory, but these are, in general, computationally more difficult. In order to provide a semblance of realism to the problem, we use some now somewhat outdated data provided in Table 7 of Green and Broadhead (1965). We begin by assuming we have a fleet of 300-, 400-, and 500-ton seiners. The capacity of the fleet is calculated in Table 1.

The capacity for each size class of boat is an input in the production function. We also need to supply as inputs to the production function some raw material in the form of fish. Let us say that we are limited to 90,000 tons of yellowfin tuna and 120,000 tons of skipjack tuna. Then the objective of production is to maximize profits

TABLE 1.—The capacity in tons of a hypothetical tuna fleet in terms of various size classes of fishing boats.

Size of boat (tons)	Size of fleet (No. of vessels)	Capacity of each boat (tons)	Annual capacity of each boat (tons)	Total capacity for fleet (tons)
300	20	273	1,173	23,460
400	60	364	1,419	85,140
500	20	455	1,592	31,840

by maximizing the objective function: $Z = 8.65H_{11} + 7.32H_{12} + 10.66H_{21} + 9.01H_{22} + 7.75H_{31} + 6.53H_{32}$ where the H_{ij}'s correspond to the ith boat size ($i = 1, 2, 3$; where the integers refer to 300-, 400-, and 500-ton boats, respectively) and the jth species ($j = 1$ is yellowfin tuna and $j = 2$ is skipjack tuna). The coefficients in the objective function correspond to the weighted average profit per ton for the jth species caught by the ith boat as deduced from Green and Broadhead. Now with respect to the allocation of two scarce inputs—the capacity of various size vessels in the fleet and the catchable stock of the two species—to the production process, the capacity of the fleet generates the following set of constraint equations:

$H_{11} + H_{12} \leqslant 23{,}460$ tons (capacity of small boats)

$H_{21} + H_{22} \leqslant 85{,}140$ tons (capacity of medium boats)

$H_{31} + H_{32} \leqslant 31{,}840$ tons (capacity of large boats)

whereas the stock inputs (viz. the catch quotas) generate the following set of constraints:

$H_{11} + H_{21} + H_{31} \leqslant 90{,}000$ tons ("quota" of yellowfin tuna)

$H_{12} + H_{22} + H_{32} \leqslant 120{,}000$ tons ("quota" of skipjack tuna).

Because different size boats catch different proportions of yellowfin and skipjack, the ratio of these species in the catch of each size class of boat is essentially a function of the configuration of the boat and its equipment. We can thus consider the ratio of skipjack to yellowfin as a technological characteristic of the boat's size class and in order to maintain the character of the technology, we use the percentages of yellowfin in the catch as given by Green and Broadhead (300-ton boats, 57%; 400-ton boats, 48%; and

TABLE 2.—Optimal allocation of skipjack and yellowfin tuna in tons of fish to various size classes of fishing boats.

Species of tuna	Size class of boat			Total
	1 (300 ton)	2 (400 ton)	3 (500 ton)	
Skipjack	10,112	43,886	18,511	72,509
Yellowfin	13,347	41,253	13,328	67,928
Total	23,459	85,139	31,839	140,437

500-ton boats, 42%) to obtain the yellowfin:skipjack ratios of 1.32, 0.94, and 0.72, respectively, thus yielding the technological constraints:

$$H_{11} - 1.32H_{12} = 0$$
$$H_{21} - 0.94H_{22} = 0$$
$$H_{31} - 0.72H_{32} = 0$$

Table 2 gives the maximization of the objective function which yielded $1,248,835 in tons of fish. The optimal solution then indicates that in the process of production, the entire capacity of the vessels was utilized. Because the catchable portion of the stocks was greater than this capacity, 22,070 tons of yellowfin and 47,489 tons of skipjack were unused by the fishery (slack variables). Note also that the catch of skipjack is greater than that of the more valuable species, yellowfin, because of the technological constraints enforcing the lower yellowfin:skipjack ratios in the more numerous larger boats. The imputed marginal values, the so-called shadow prices of a ton of yellowfin and skipjack are, of course, zero because the capacity of the stock to produce these quantities of fish was not reached; but, however, the capacity of the vessels was reached and, therefore, the marginal value of an extra ton capacity on the 300-, 400-, and 500-ton boats is imputed to be $8.08, $9.81, and $7.04, respectively. These shadow prices are simply the weighted average profits for each size class, e.g.:

$$\$8.08 = \frac{10,112}{23,459}\,7.32 + \frac{13,347}{23,459}\,8.65$$

Perhaps of even greater interest is the way in which the various production inputs interact with one another. For example, in this particular problem, we could increase the yellowfin and skipjack catchable population constraints *ad infinitum* without changing the nature of the optimal solution. But if we were to reduce the catchable population of yellowfin tuna from 90,000 tons to 67,930 tons or skipjack from 120,000 tons to 72,510 tons, we would eliminate the yellowfin and skipjack slack variables, respectively, and these would no longer be in the optimal solution. Putting it another way, insofar as this particular problem is concerned, the nature of the solution, in terms of, for example, those variables to which some monetary value greater than 0 would be imputed, would not change until the catchable population of yellowfin dropped below 67,929 tons or skipjack to below 72,510 tons. The point of this is that (again insofar as this particular problem is concerned) we are not going to change the nature of our optimal solution for any catchable populations of yellowfin >67,929 tons or of skipjack >72,510 tons. This means that it may not be necessary to be concerned with precise estimates of the catchable population if the catchable population is, as in this case, much larger than the lower bounds for changing the solution. This reflects, within the scope of the model, the bounds within which changes in the catchable population will have no effects upon the components of the objective function. This demonstrates, in an analytical way, that population dynamics theory may offer solutions that are, in some instances, apparently more precise than that which is needed. In other words, we frequently postpone resource decisions to obtain a certitude in our estimate, which would not change the optimal solution of the input-output process. This postponement is almost never without social costs which may be substantial.

Now with respect to modifying the fleet capacity, we can, given the stock constraints, increase the capacity of the small boats to 62,250 tons or decrease it to 0 tons. If we exceed the upper bound then this means that we need to catch at least 38,790 additional tons of fish and, of these, 57% must be yellowfin amounting to an additional catch of 22,110 tons of yellowfin. But if we catch this additional quantity of yellowfin, we will use up our 90,000 tons of yellowfin, dropping the yellowfin slack variable from our solution. At the lower bound, it is obvious that if we constrain the catch of small boats to be 0,

we eliminate the variables corresponding to the catch of small boats from our optimal solution. The interpretations of the sensitivity of the 85,140-ton constraint upon the maximum catch of the 400-ton boats and the 31,840-ton constraint upon the maximum catch of the 500-ton boats are identical.

It is perhaps more subtle that the *full* utilization of the excess yellowfin tuna capacity is impossible because the 85,140 tons of fish that would be caught by the 400-ton boats consists of $85,140 \times 0.48 = 40,867$ tons of yellowfin tuna (the 0.48 is the appropriate technological constraint). To use up the yellowfin tuna surplus we would need to catch roughly an additional 50,000 tons of yellowfin tuna, but if we did this we would need, by virtue of our technological constraint, to catch a total of 90,000 $(0.48)^{-1}$ tons of fish which clearly exceeds the fleet capacity. With respect to the technological constraints, we could in the 300-ton boats, for example, increase the right-hand side of the equality to 23,460, which would modify the solution by eliminating any catch of skipjack by the small boats (in other words, H_{12} would be eliminated from the optimal solution). On the other hand, we could reduce the equality to —30,967, and if we did this, the catch of yellowfin by small boats would be eliminated from the solution $[(30,967)(1.32)^{-1}] = 23,460$. The negative right-hand constraint reflects more upon the nature of the solution than reflecting any physical meaning.

It is clear that since we used all the capacity of our hypothetical fleet that any increase in profits will not induce us to catch more fish. On the other hand, by inducing a negative profit we can show that in these instances some of the boat-species combinations should not be filled to capacity (Table 3). Thus we would have to lose

TABLE 3.—The lower bound of profit and "sensitivity" for yellowfin and skipjack tuna caught by various size classes of fishing boats. The results are reported in dollars.

Species of tuna	Boat class	Profit per ton in problem	Lower bound of profit	"Sensitivity"
Yellowfin	1	8.65	—5.54	14.19
	2	10.66	—9.58	20.24
	3	7.75	—9.07	16.82
Skipjack	1	7.32	—11.41	18.73
	2	9.01	—10.02	19.03
	3	6.53	—5.58	12.01

$5.54 per ton of yellowfin to generate empty capacity space in class 1 vessels. The difference between the lower bound profit and the profit used in the problem is a measure of sensitivity. We note for example that the behavior of the fleet is most sensitive in class 3 boats where a $12.00 decline in profits would generate excess fleet capacity, or a $16.82 decline in yellowfin profit would also generate excess fleet capacity.

Now let us make an apparently slight but important modification in our problem. We will keep everything the same, but we will increase the capacity of the small boats from 23,460 tons to 65,000 tons. In the first example we were interested, primarily, in the sensitivities of our model to changes in the constraints. Now, however, it is of interest to compare the optimal solutions in the two examples (Table 4). Thus by adding an extra 42,000 tons of capacity to the small boats, we increase the skipjack catch by only 16,000 tons and the yellowfin catch by 22,000 tons. We have not, owing to the constraints, caught an additional 42,000 tons of fish. We have caught proportionately more yellowfin than skipjack, increasing the optimal solution from $1,248,835 to $1,562,133. In the second example, in contrast to the first, we have used

TABLE 4.—A comparison of optimal solutions in Example I where the capacity of the small boats is 23,460 tons and in Example II where the capacity of the small boats is 65,000 tons. The comparison shows the optimal allocation in tons of fish for each example.

	Example I				Example II			
	Boat class				Boat class			
Species	1	2	3	Total	1	2	3	Total
Skipjack	10,112	43,886	18,511	72,509	26,831	43,886	18,511	89,228
Yellowfin	13,347	41,253	13,328	67,928	35,418	41,253	13,328	89,999
Totals	23,459	85,139	31,839	140,437	62,249	85,139	31,839	179,227

up our yellowfin tuna resource and have reduced the unused portion of the skipjack resource from 47,489 to 30,769 tons. In addition, we have 2,749 tons of empty capacity in the small boats. This excess capacity is enforced, to a large extent, by the technological constraints, and we can see that these modifications would enable utilization of the empty space with skipjack tuna. Thus we can formulate, in a programming context, the relation between the inputs and outputs of the fishing process. If we agree that the management process requires the kinds of information that are required in the programming problem, then we can see that we have been collecting the wrong kinds of information on our fisheries.

To sum up, then, we have discussed the production function from a linear-programming point of view. We have picked two possible examples out of an infinitude of possible examples. The particular examples we have chosen may be criticized from the point of view of their immediate applicability to real situations. This criticism is correct and indeed it is quite an important criticism which simply reflects that in these tuna fisheries and most of the other fisheries in the world, we simply neither have nor collect the kinds of data that we need to enter into an analytic evaluation of what is perhaps the most critical of fishery management problems, the allocation of fishery resources among various user groups throughout the time stream. This is not because these data do not exist; it is because, in general, explicit attempts have not been made to gather these sorts of data. It is a contradiction to deny the usefulness of utilizing the physical metric for managing fisheries and to not provide mechanisms for obtaining the kinds of data that are required to manage the fisheries in the appropriate way, in the value metric.

The point, then, of demonstrating the linear-programming technique is to (1) call attention to a powerful allocation tool which can be used for guidance in, for example, a serious contemporary tuna problem, the allocation of the tuna catch among the nations; (2) highlight the important difference between the inputs of the fishing process and the fishing effort used in population dynamics; (3) point out the nature of sensitivity in a programming context which can show, for example, that when we examine the entire productive process that, given the right kinds of economic data, we can think of managing stocks in terms of, say, an upper and lower bound on catch which could free research effort, for example, to other productive endeavors; and (4) finally, because of recent confusion on the subject, suggest that the term fishing effort be utilized only in the context in which it is defined in the population dynamics literature and that the term fishing inputs be reserved for the more general connotation of "fishing effort."

INTERPRETATION OF FISHING SKILL

Now let us look at the input process in a little more detail. When we do this we have to admit that we can, having established the definitions of fishing effort and fishing inputs, especially if we restrict our consideration of management to manipulating physical quantities of the catch, relate at least some but, in general, not all of the fishing inputs to fishing effort through the appropriate catchability coefficient. This enables the dynamicist to have comparable measures of the abundance of fish from time-space point to time-space point. Again the adjustment of estimates of abundance to common units through the computation of fishing power is well treated in the literature, and we will not belabor it here, except to note that fishing power is almost always calculated on the basis of some usually single physical feature of the fishing vessel such as engine horsepower, etc., or simply on empirical differences in the catch-per-nominal-effort that is obtained by the fleet. Differences in fishing power are certainly more complicated than comparisons among the physical attributes of the fishing vessels would indicate. A considerable portion of the variability in fishing power among fishing units can be attributed to variability in the skill of the fishing skipper. This assertion is subsumed in Figure 1.

Figure 1 is hypothetical and shows that the quality of fishing skippers could be a more important determinant of the "quality" of a fishing operation than the physical characteristics of the boats. We might guess that boats that are phy-

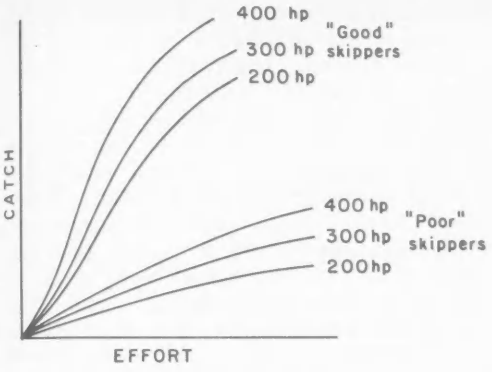

FIGURE 1.—Hypothetical relation between catch and effort for boats of varying horsepower and for "good" and "poor" skippers.

sically different in some important index in a ratio of say 2:1 may exhibit a range in catch-per-input where the best boat is, say, 10 or more times better than the poorest boat. The greater effectiveness of some boats over other boats can in large part be attributed to the skill of the skipper. This is ignored in many analyses primarily because this question of skill has never been appropriately formulated. In this section, we begin to develop some examples which contribute to the rudiments of analysis of the behavior of the skipper as an input to the production function—in terms of how a skipper perceives the fishing environment—and then mention the problem of the utility that the skipper places on the various signals that he obtains from the environment. We make a point of stressing that the relation of the input vector to the output vector in the fishing process is usually considered to be deterministic by students of the fishing process. Another approach is to use an average vector for inputs and assume an average vector for outputs. Unfortunately, it is unlikely that fishermen perceive the decision environment as either deterministic or average and we make use of this observation in our additional considerations.

In order to demonstrate these points we will construct a branch of a very simple decision tree which can serve as a framework for future analysis. The branch of the tree is shown in Figure 2. This is the skipper's decision environment. Nature deals the skipper good fishing, Θ_1 or poor fishing, Θ_2. The skipper has an opportunity to take a glimpse at the environment. This interpretation of the glimpse is denoted by $P(\hat{\Theta}_i \mid \Theta_j)$ where $\hat{\Theta}_i$ is his guess of Θ_i (j does not necessarily have to equal i). If the skipper guesses $\hat{\Theta}_1$, then he commits himself to a fishing operation, but if he guesses $\hat{\Theta}_2$, he moves to a less risky area and fishes. In this less risky area, nature deals new fishing conditions Θ_1' and Θ_2'. The reward for any particular fishing action is specified in Figure 2. We wish to use this model to show how chance enters the decision process.

We set

$$\begin{aligned} P(\Theta_1) &= 0.2 \\ P(\Theta_2) &= 0.8 \\ P(\Theta_1') &= 0.8 \\ P(\Theta_2') &= 0.2 \end{aligned}$$

and examine three conditions:

Condition I

The skipper is perfectly skilled and thus $P(\hat{\Theta}_1 \mid \Theta_1) = P(\hat{\Theta}_2 \mid \Theta_2) = 1$ and $P(\hat{\Theta}_1 \mid \Theta_2) = P(\hat{\Theta}_2 \mid \Theta_1) = 0$. The expected value of the branch

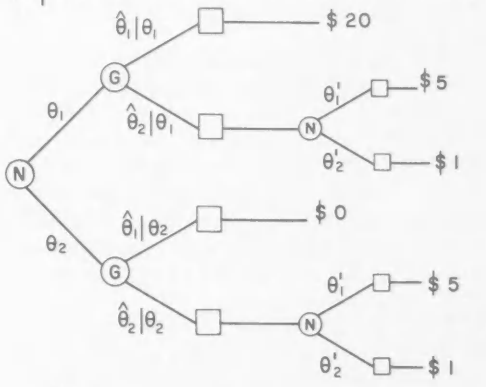

FIGURE 2.—Branch of decision tree showing various events and payoffs. (For a discussion of decision analysis see Raiffa, 1968.)

is \$7.36 with a measure of entropy of 130 centibits. (Entropy is defined in the usual way, but measured in centibits rather than in bits owing to the relatively low degree of "randomness" in these hypothetical examples.)

Condition II

The skipper is quite skilled and thus $P(\hat{\Theta}_1 \mid \Theta_1) = 0.9, P(\hat{\Theta}_2 \mid \Theta_1) = 0.1, P(\hat{\Theta}_2 \mid \Theta_2) = 0.9, P(\hat{\Theta}_1 \mid \Theta_2) = 0.1$ (say). The expected value of the branch under this condition is \$6.71, and a measure of its entropy is 172 centibits.

Condition III

The skipper is unskilled and thus $P(\hat{\Theta}_i \mid \Theta_j) = 0.5$ for $i = 1,2$ and $j = 1,2$. The expected value of the branch under this condition is \$4.10, and a measure of its entropy is 209 centibits.

It is important to observe, in respect to the first example, that if nature dealt the Θ_i's with probability of 1 or 0 then entropy would be 0. Nature has not, in our example, chosen to deal the Θ's deterministically and, therefore, 130 centibits is the lower threshold of entropy, given that probabilistic behavior of nature remains the same.

Now, we note several interesting features of this analysis which are capable of many simple extensions. First, we have distinguished between the contribution to entropy made by the behavior of nature and the behavior of the fishermen. Second, we have quantified the randomness in the decision problem by measuring the randomness in bits and thus have the opportunity to quantify the required skill of the skipper; because when nature deals a low-entropy probability structure, relatively less skill is required to achieve equivalent results. Third, we can valuate the skipper's decision process as an input to the production function. For example, under Condition III an unskilled skipper can produce, on the average, \$4.10 worth of fish in a 209-centibit environment, but a quite skilled skipper [skill being measured by $P(\Theta_i \mid \Theta_j)$] can *by his skill* reduce the entropy 37 centibits. The 37 centibits being a difference between entropies is thus a measure of information, and in this example 37 centibits of information are worth \$2.61 or roughly 7 cents per centibit. A perfectly skilled skipper reduces entropy an additional 42 centibits, the additional information yielding 65 additional cents, or about 1.5 cents per centibit. In other words, in this example, the information accrued in moving from unskilled to quite skilled is about the same as that accrued in moving from quite skilled to perfectly skilled, but the value of a unit of information is 4 times greater in moving from unskilled to quite skilled than a unit of information acquired when moving from quite skilled to perfectly skilled.

DECISION CRITERIA

Thus, we have considered a model of the way in which the skipper "processes" signals from the fishing environment where the quality of his processing ability is measured relative to nature-generated entropy in the decision environment. We must now consider how the skipper valuates the signal and the criteria that he places upon these signals. First, consider what might be a traditional approach of where to fish. In this approach we have a field of expected catches and upon examining this field we advise the skipper to fish at the location where the expected catch is highest. A second approach is to examine the field of space-time points and consider the distribution of catches at each space-time point. Let us consider a simple aspect of this problem; two space-time points A and B, at which the fisherman's perception of the catch is that it has an approximately normal distribution. Figure 3 shows these two distributions. The figure also indicates the point on each distribution below which the fishing operation will lose money. If we look at only the expected catch, we would advise fishing at A. But if we examine the risk (that is, $\int xf(x)\,dx$, evaluated from $-\infty$ to the break-even point) we note that fishing at B will minimize risk, and if this were our criterion we would fish at B. We should note further that the fish-

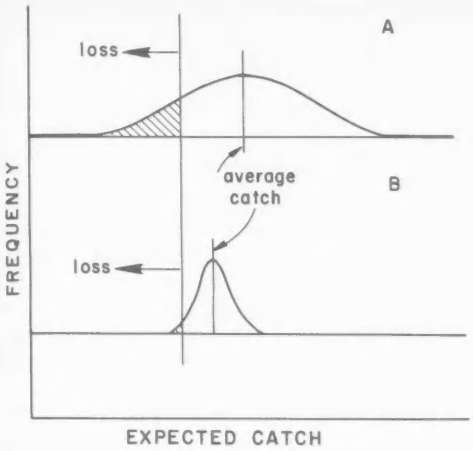

FIGURE 3.—The distribution of catch at two locations showing the average catch and the loss region.

erman samples the distribution dealt by nature and his sample can be biased and vary in precision. His perception of the correct action depends upon his view of how many times he can sample these distributions. This is clear because if the fisherman has only one chance to go fishing, he should choose B to minimize his risk, but if he has many chances to go fishing, he should choose A to maximize his gain since the sampling risk will be decreasing inversely proportional to the square root of the number of chances that the fisherman has.

A reasonable criterion for choosing a fishing location might be the expected gain less the expected loss; e.g.,

$$\int_a^b xf(x)\,dx - \int_a^B xf(x)\,dx$$

where $f(x)$ is the distribution function of the fisheries earnings, a is the minimum value of this function, b is the maximum value, and B is the break-even point. Note that this general form can be written in several alternative ways. But even the establishment of such a criterion is not sufficient to measure the skipper's behavior. We need to know the utility that the skipper places in any value of the criterion.

ACKNOWLEDGMENTS

It is a pleasure to contribute this paper in honor of Dr. O. Elton Sette who has done so much pioneering work in fishery biology and has provided me with many stimulating discussions during the last several years.

I would like to thank James Joseph of the Inter-American Tropical Tuna Commission and Paul Adam of the Organization for Economic Cooperation and Development who encouraged me to write this paper. James W. Balsiger kindly read the manuscript. Much of this paper was written under the Sea Grant, Norfish program, while I was with the Center for Quantitative Science in Forestry, Fisheries and Wildlife at the University of Washington.

ADDENDUM

The reader interested in applications of decision theory should examine "Marine decisions under uncertainty," by John W. Devanney III, Cornell Maritime Press, 1971, which was discovered while the present paper was in proof.

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UNDERGRADUATE EDUCATION OF FISHERY SCIENTISTS[1]

WILLIAM F. ROYCE[2]

The requisite preparation and training for the profession of fishery scientist[3] has received much attention from faculties giving instruction related to fishery problems and from a number of people who have examined the educational problem in some depth, notably Deason (1941), McHugh (1968), Paulik (1968), and Carlander (1970). Almost everyone has been dissatisfied with the curricula available. Those of us who are concerned are well advised to ask what we can do to improve our preparation of fishery scientists for their roles in society as scientists and as citizens.

The traditional approach to fishery science was through training in natural history, especially in ichthyology and limnology. The first special courses in fisheries in North America were developed in aquaculture and fishing. Later, courses were offered in the biology and ecology of fishes and in fishery management. It was recognized generally, however, that most of the training of fishery scientists should be in biology and a degree in fisheries was equated with a degree in either biology or zoology by many agencies that employed fishery scientists.

The traditional approach is now being challenged from many directions. The problems of public fishery management are only part of the immensely complex problems of environmental management, the solution of which involves predominantly the management of people. The proliferation of specialized courses in biology causes many fishery students to wonder whether most of them are useful. The diversity of fishery jobs stimulates others to inquire what set of courses should be taken for each. It is now accepted generally that an undergraduate biology major is not the best preparation for most fishery jobs, and the basic question is asked—What is the best education for each kind of fishery job?

ROLE OF FISHERY SCIENTISTS

The common division of fishery science into management and research fails completely to indicate the diversity of jobs that are filled by fishery scientists. Carlander (1959) in his survey of technical fishery careers used the categories: (1) fish culture; (2) management; (3) survey and trouble shooting; (4) research; (5) education; and (6) administration. Later (1970) he listed a sampling of fishery courses and included a number of additional subjects that might well be job categories: (1) pond and lake management; (2) hatchery management; (3) fishery technology and economics; (4) pollution biology; and (5) population dynamics. Obviously, the category of fishery technology can be separated into commercial fishing and fish processing technology and the category of fish culture can be extended to include shellfish culture.

A much more diverse group of categories is included in Hall's (1969) review of fishery occupations on an international basis. He considers that most of the personnel engaged in the following fishery activities require a high degree of special fishery knowledge: (1) seagoing and other personnel in the primary sector; (2) processing, distribution, and marketing personnel; (3) management, government administration, enforcement and development personnel; (4) research and education personnel; and (5) economists and statisticians. In addition he lists

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[3] Included in this category are all fishery resource workers who normally are required to have a baccalaureate degree or higher for the job they hold.

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ancillary industries associated with the construction of gear, vessels, processing equipment, and harbors and reservoirs that require personnel with an awareness of fishery problems. Obviously, only part of the occupations in both lists requires a science degree—the topic of this discussion.

Further, an examination of the publications of any major fishery agency reveals many diverse research topics, each of which could be discussed adequately by an individual only after years of specialized experience in graduate school or on the job. For example, recent issues of the *Journal* and *Bulletin* of the Fisheries Research Board of Canada include lengthy articles in each of the following areas of study: (1) biochemistry of pesticides, heavy metals, etc.; (2) fish and invertebrate physiology; (3) animal behavior; (4) ecology; (5) population dynamics; (6) life histories of animals of many phyla; (7) ichthyology; (8) genetics; (9) hydraulic engineering; (10) marine biology; (11) limnology; (12) oceanography; (13) microbiology; (14) pathology; (15) mathematics; (16) resource economics; and (17) fishery business administration.

This list could be expanded considerably but with little reinforcement of the conclusion that specialists on many topics contribute to fishery knowledge and aid in fishery decisions. Obviously, many problems must be studied by teams of experts who can apply their individual skills to a problem in which they share a common interest and concern.

Still further evidence of diversity may be found among employers of fishery scientists. Government fishery agencies are the principal employers, but nonfishery agencies and industry appear to be offering more and more jobs. Outdoor recreation agencies; water control and water quality agencies; soil, range, and forest resource agencies; and industries that use water are finding increasingly that they have enough fishery problems to warrant hiring fishery scientists. In addition, the fishery agencies are finding that the management of the fishery resources requires that they participate frequently in decisions about the use of water and land. It is apparent that many fishery scientists need at least to be aware of if not expert in the problems of using other natural resources.

THE CHOICE OF BACCALAUREATE DEGREE, MASTER, OR DOCTORATE

Soon after an aspiring fishery scientist has embarked on his education he faces a decision about when to stop and seek a job. He will probably be advised to seek graduate work if his scholarship is adequate and if he can finance it. If he does he will be a part of the one-fifth of the biologists who have recently sought advanced degrees (Terman, 1971). The brilliant student can get a fellowship or assistantship, so his decision may depend on whether he wants to spend the extra time; but to other students graduate work may require a major sacrifice. Will the added breadth of knowledge or specialization be worth the time and cost?

The roles of fishery scientists are not clearly separable according to terminal degree attained by them, but most of those with a baccalaureate are in fishery management and most of those with a doctorate are in teaching or research (Table 1). Many of those with a baccalaureate, however, are engaged in research or administration. Those with a master are engaged extensively in research, management, and administration; but a larger proportion of them than of the other two groups are in research and administration.

The divisions among fishery research, management, and administration are blurred, however, in other ways. All three require an ability to investigate problems but research will probably involve the solution of sophisticated scientific problems; management, a mixture of scientific, technical, and social problems; and administration, a mixture of social, economic, and political problems. All three require an understanding of the general environmental problems of our society, but these will probably be of greatest concern in administration. All three require an ability to communicate, but with different audiences. Additional blurring occurs because most fishery scientists divide their time among research, administration, and management or teaching.

TABLE 1.—Breakdown of respondents from Pacific Fishery Biologists by types of professional activities and fishery, highest degree attained, major subject, employer, and institution of origin.[1]

Item	Duties ≥40%[2]					Type of fishery ≥60%[3]	
	Fishery research	Fishery management	Teaching	Administration	Others	Recreational	Commercial
N 324	116	100	19	95	33	117	134
Highest degree							
B.S. 183	60	74	0	26	10	73	76
M.S. 85	33	22	1	32	11	34	36
Ph.D. 54	23	3	18	16	3	9	22
Years since last degree							
<10 126	57	47	10	19	17	53	46
10-29 115	38	35	5	36	10	40	52
>19 79	18	17	3	40	6	22	36
Major subject							
Fisheries 225	82	72	12	64	22	84	98
Biology, zoology 73	27	22	6	22	6	27	26
Employer							
NMFS 48	33	4	0	13	2	1	42
BSFW 24	5	3	3	8	7	11	4
State fisheries 154	46	78	0	41	9	79	49
Nonfisheries 30	2	8	1	14	9	13	4
Canada fisheries 14	4	5	0	7	1	4	8
Universities 32	13	0	15	7	2	4	14
Industry 7	4	2	0	1	2	3	1
Institution							
Univ. Washington 81	38	21	6	26	1	14	54
Oregon State Univ. 65	12	33	2	19	10	33	18
Other large univ. 73	27	21	3	22	5	30	29
Two or more univ. 63	23	12	7	23	10	23	19

[1] Nonresponses and certain minor categories have been omitted.
[2] The respondents who indicated a division of duties of 60-40 or 50-50 are included in two categories.
[3] The respondents who indicated a division between the two fisheries of 50-50 have been omitted.

Another separation of functions is between investigative and decision making activities. It may be assumed that research is predominantly investigative, administration is predominantly decision making, and management is both investigative and decision making.

In actual practice it appears that a majority of the fishery scientists in western North America have no more than a baccalaureate and are engaged in fishery management and administration. The responses (324) to a recent questionnaire to members of Pacific Fishery Biologists (PFB) indicated that 56% had only a baccalaureate degree, 26% had added only a master, and 17% had a doctorate. When queried about their activities 36% of the respondents said they were engaged in fishery research for 40% or more of their time, 31% in fishery management, 29% in fishery administration, 6% in teaching, and 10% in other activities, most of which were water management. (Some said they were engaged for 40% or more of their time in each of two activities and hence were counted twice in the above breakdown.)

It should be noted that the overall projections of supply vs. demand for Ph.D.'s indicate an oversupply for the needs of basic research and teaching and an expectation by many of a search for employment elsewhere (Cartter, 1971; Terman, 1971). The natural resource agencies and offices should expect an influx of Ph.D.'s trained in other areas during the 1970's.

The role of a person with a terminal master degree appears to be primarily in research and administration. A higher proportion of the members of PFB with a master degree than of those with either a baccalaureate or doctorate were engaged in administration, and the proportion of them that were engaged in research was nearly as high as the proportion of those with a doctorate so engaged. The master's training provides either the breadth of education that gives a person a wide choice of jobs or a special education for a particular job. It appears to be

especially useful to the person who works after earning a baccalaureate and then decides to obtain more education for clearly defined reasons.

Thus, the demand for fishery scientists will probably remain, as it has been, predominantly for baccalaureates; and this demand will coincide with the inclination of a majority of students to earn no more than the baccalaureate. The implications for the fishery educator seem clear —prepare an undergraduate student for a job if he intends to terminate his formal schooling with a baccalaureate and prepare him for graduate work if he plans immediately to work for an advanced degree. "Preparing a student for a job" does not mean training him extensively in techniques that he could learn as well or better on the job; rather it means preparing him as a scientist and citizen so that he can choose among a reasonable number of job alternatives and progress rapidly in the job that he finds.

SURVEY OF OPINION REGARDING FISHERY CURRICULA

Opinions and criticism of fishery curricula are frequently expressed by two groups of people, both of which should be regarded as biased: fishery faculty and employers. Fishery faculty tend to be oriented toward basic research and the necessity for doctorate degrees, which most of them have. They may even suggest that persons who get only a baccalaureate degree are likely to be only research technicians. Employers are necessarily concerned with the immediate problems of getting a job done and having employees who can do the job well with a minimum of added training. They are usually less interested in the capability of a new employee to grow in skill and take over major responsibility at a later date. Consequently, it was deemed useful to obtain opinions from others.

During the spring of 1971 it was possible to sample the opinions of members of the PFB with respect to fishery curricula. Membership in the organization, according to the bylaws, is "limited to graduates of universities of recognized standing who possess a degree in the biological sciences who are professionally engaged in fishery biological research and who have completed at least one year's cumulative service in research with some organization following graduation provided that employment in an organization in one of the following areas shall be necessary for membership: Alaska, British Columbia, Washington, Oregon, California, Idaho, and Hawaii." The organization included 751 active members in May 1970, a considerable fraction of the estimated 5,500 fishery biologists who were employed in the United States on July 1, 1970 (Martin, 1971).[4] The members were affiliated with one provincial and six state departments of fisheries or fish and game, two Federal fishery agencies, three Canadian fishery agencies, nine nonfishery government agencies, seven nonfishery industries with environmental problems, twelve colleges and universities, and the California Academy of Sciences (Table 1). Either notably absent or scantily represented were fishery scientists employed either in aquaculture or in the fishing industry. Probably underrepresented were fishery management biologists because of the requirement by PFB for professional engagement in fishery research. Subject to these qualifications the organization probably represented quite fairly at the time the fishery scientists in the western United States. Also canvassed were persons on the mailing list for the Northwest Fish Culturists Conference and student groups at the University of Washington.

The opinions about most useful and least useful subjects required somewhat arbitrary and subjective classification of the subjects into not more than 10 groups, as follows:

0) Function and methods
1) Biological sciences
2) Chemistry, physics, and mathematics
3) Natural resource sciences and management
4) Social sciences
5) Engineering and technology
6) Administration
7) Humanities and liberal arts
8) Communications
9) Other fields

[4] Martin, R. G. 1971. Potential employment market. *In* Items for fishery scientists from the Sport Fishing Institute. Jan.-Feb. 1971.

In the interest of saving space, no more than five subjects were coded for any one reply. When two or more subjects listed under the same code number were named, that code number was listed two or more times. When the answer was "all biology courses," however, the biology code number was listed once.

Further comments were classified in groups under the following general headings:

0) Miscellaneous comments or no comment
1) Increase practice and experience
2) Improve quality of courses
3) Improve curriculum
4) Help select and understand jobs
5) Arrange continuing education

COMPARATIVE USEFULNESS OF SUBJECTS

After the data had been coded, they were sorted and listed by the computer. The number of times that each subject was mentioned by respondents in each category was determined, and the total was computed as a percentage of the number of respondents.

The percentage of respondents that mentioned a subject as most useful, as least useful, or one that the respondent wished he had added to his college courses or taken in greater depth is regarded as an index of the usefulness of the subject. Inclusion in the most useful or the least useful category depended on inclusion of the subject in the respondent's training. The subjects of average usefulness were not mentioned, and there is no way of considering such a status from the data. The last class of subjects, subjects that the respondent wished he had added or taken in greater depth, is, of course, not limited to subjects taken in the university; but presumably many respondents would think first of subjects that they had taken but not as completely as they might have.

One of the difficulties in evaluating answers was the distinction between a general course, for example, in biology, and a collection of advanced courses that might also be called by the same name, in the example given, biology. Some respondents made this distinction clear; others did not, especially some who had taken their college work many years ago.

The outstanding characteristic of the responses is the inclusion of almost every subject among someone's most useful subjects and someone else's least useful subjects. It appears that subjects considered by most people to be very useful were ranked as the least useful by a few people who had special difficulties with a course, such as a quarrel with the instructor or a bad grade. Accordingly, it is felt that a designation of a subject as least useful by 1 or 2% of the respondents is not of particular significance unless the course was one that relatively few respondents would be expected to take.

The rating of subject groups is shown in Table 2. The groups are ranked starting with the one that was considered to be most useful by the greatest percentage of respondents and ending with the one that was considered to be least useful by the greatest percentage of respondents. Only the top twelve in any category have been ranked. The results are discussed in the following paragraphs.

The ranking of English-scientific writing as the most useful group of subjects may surprise many scientists, especially the younger ones who are preoccupied with learning science, but undoubtedly it reflects the broad experience of the applied scientists, who have repeatedly faced the need to communicate their findings. Only a few respondents rated these subjects as the least useful, and some of these specified that they objected to English literature or creative writing courses.

Public speaking, another method of communication, ranked eleventh among the subjects listed as the most useful and fifth among the subjects that should have been added or taken in greater depth. Those rankings probably reflect the failure of many fishery scientists to take public speaking and their general need for it later.

Communication in a foreign language was at the other end of the scale, however, first among the courses rated as least useful. Such courses are apparently a waste of time for most students but are needed by a few.

The next surprise for those who consider fisheries as essentially biology is the second place

TABLE 2.—Percent of responses naming undergraduate subjects as most useful, least useful, or one that should have been added or taken in greater depth.

Subject group	Most useful		Least useful		Should have been added or taken in greater depth	
	% of respondents	Rank	% of respondents	Rank	% of respondents	Rank
English, scientific writing	44	1	3	--	21	2
Biostatistics, population dynamics, computer use	34	2	2	--	44	1
Zoology	30	3	2	--	1	--
Fisheries, fishery biology	27	4	1	--	5	12
Mathematics, calculus	27	5	4	11	20	3
Chemistry, inorganic	23	6	12	4	5	--
Oceanography, limnology, pollution study	16	7	0	--	12	4
Ecology	16	8	0	--	8	10
Ichthyology, systematics	16	9	3	--	2	--
Physiology, cytology, embryology, morphology, etc.	13	10	6	8	9	9
Public speaking	10	11	1	--	12	5
Fishery management	10	12	1	--	4	--
Aquacultural sciences	8	--	4	12	7	11
Economics	4	--	4	--	12	6
Administration	0	--	1	--	12	7
Physics	6	--	5	10	2	--
Agriculture	0	--	5	9	0	--
Chemistry, organic	2	--	6	7	5	--
Advanced biology	2	--	6	6	3	--
Botany	7	--	7	5	4	--
Social sciences (except economics)	1	--	14	3	10	8
Humanities, liberal arts	3	--	16	2	4	--
Foreign language	2	--	21	1	2	--

ranking of biostatistics-population dynamics-computer use and the fifth place rating of mathematics-calculus. Both of these subject groups ranked even higher among those that the respondents wished they had added or taken in greater depth.

Biology, botany, and zoology courses varied greatly in their usefulness. General zoology ranked third among those listed as the most useful, ichthyology and systematic zoology ranked ninth, and a group of advanced zoology courses ranked tenth, largely because of the inclusion of the physiology of resource animals. Other advanced zoology courses and botany were more frequently among those listed as the least useful than among the most. Many respondents noted these as "too specialized" or "memory type" courses that they objected to. On the other hand, a few people rated them most useful.

Chemistry courses were viewed much like biology courses. The general courses were ranked relatively useful, but the advanced courses were rated not useful by more respondents than those who considered them useful.

The natural resource sciences also varied greatly in their usefulness. Fisheries and fish biology courses ranked fourth among those listed as most useful and fishery management twelfth. Aquacultural science, including pathology, parasitology, nutrition, and genetics as applied to fishery resource animals, varied greatly in usefulness (sample population was underrepresented in aquaculture). Apparently these are specialized courses, needed only by a few people. Other natural resource sciences, such as wildlife science or management, forestry, soil science, and land management, also varied in their usefulness.

The opinions about the usefulness of the social sciences were anomalous. Almost all of the social sciences except economics were rated least useful if they were mentioned and yet many respondents wished they had taken more social science courses. The apparent explanation for

this dichotomy is the current upsurge in recognition of the social problems and the lack of relevance of the earlier social science courses. Economics as a general subject was also judged least useful by some respondents, but resource economics was valued by many and was ranked sixth among those that respondents wished they had added or taken in greater depth.

Less divergent were the opinions about humanities and the liberal arts. This set of subjects ranked second among those listed as least useful. A very small proportion of the respondents valued them highly, and some explained that courses in music and literature were especially useful in their life but not in their professions.

Courses in administration were rarely mentioned as useful but ranked seventh among the subjects that the respondents wished they had taken. Apparently such courses were seldom taken by the respondents but are needed, especially by many of the older fishery scientists.

VOLUNTARY OPINIONS REGARDING THE CURRICULUM

The respondents were asked to comment freely on the training of fishery scientists, and about one-third did so. The opinions were classified and the categories ranked (Table 3).

Most of the opinions expressed related to the need for extending and improving the curriculum. These include six of the eight items enumerated in Table 3, and these eight items include all comments mentioned by more than 2% of the respondents. The other two groups of comments indicate a desire for greater relevance and more practice and experience.

The prevailing views about improving the curriculum almost always suggested that something should be added but rarely suggested what should be eliminated. It follows that more effort should be made to relate the curriculum to future roles of fishery scientists as well as to provide ways of acquiring the courses used by only a small proportion of the scientists through night school, seminars, or home study.

TABLE 3.—Voluntary opinions regarding the curriculum expressed by respondents and their ranking.

Opinion	Percent
Develop more technical skills	8
Develop more communication skills	7
Develop more business, administration skills	6
Include more environmental courses	6
Have greater relevancy to real problems in courses	6
Increase practice and experience	6
Have less specialization	5
Emphasize scientific methods	5

PROPORTION OF SPECIALIZED FISHERY COURSES IN THE CURRICULUM

The members of PFB were also asked for their opinions about the proportion of specialized fishery courses in the curriculum in various years with various terminal degrees.

The replies were highly varied, but the average opinion (Table 4) was that the beginning curriculum should contain very few specialized fishery courses and that the final years should contain 50 to 60% specialized fishery courses. The final years are, of course, the junior-senior years of the baccalaureate program and the graduate years of the master and doctorate programs. Clearly the average opinion indicated a different upper class curriculum for the student who ends with a baccalaureate than for the student who plans graduate work at the outset.

TABLE 4.—Average opinions of the percentage of the fishery curriculum that should be comprised of specialized fishery courses.

	Terminal degree		
	B.S.	M.S.	Ph.D.
N	279	209	195
Lower class	16	10	10
Upper class	52	27	24
Graduate		56	59

GROUP COMPARISONS

The diverse opinions about the subjects suggest immediately an inquiry into the relation of the subjects' usefulness to the respondents' professional activities. The respondents can be divided into groups according to position, title, employer, activity, kind of fishery, final degree, major topic of study, and number of years since last degree (Table 1). The groups that can be

chosen by students during their undergraduate years deserve special examination.

Highest Degree

A major decision that a student should make sometime during his upper class years is whether to continue with graduate work. In the past these choices were probably between research or teaching and management or administration, but the careers have not been as neatly divided, nor are they likely to be in the future as more Ph.D.s go into management and administration.

Respondents holding baccalaureate and doctorate degrees differed primarily in their opinions regarding the basic vs. applied sciences. A higher proportion of those with a doctorate degree than of those with a baccalaureate rated biology, mathematics, and foreign language as their most useful subject. More would have added advanced biology, mathematics, and geology. More would improve the curriculum by giving more attention to scientific methods and less to specialization. A higher proportion of those with only a baccalaureate rated fisheries-fishery biology, fishery management, wildlife science, and biostatistics-population dynamics-computer sciences as their most useful subject, and a higher proportion would have added ecology, fisheries-fishery biology, administration, English composition, and public speaking. They suggested especially increased practice or experience and addition of communication and administration skills to the curriculum. The average opinions of those with a master as their highest degree were frequently intermediate between those with a baccalaureate and those with a doctorate except that a higher proportion of them listed advanced biology, advanced chemistry, physics, and forestry as the least useful subject and would have added economics and administration more often than either of the other groups. A higher proportion of them also suggested improving the curriculum by adding environmental courses.

Activity

The members of PFB were asked in the questionnaire to indicate the proportion of time spent in research, management, teaching, administration, or other activities. Almost all divided their time between two or more of these categories, and it was decided to separate the opinions of those who said they were devoting 40% or more of their time to any one activity. These activities might be chosen by the student; therefore, the professional opinions would be useful to him.

The researchers valued quantitative methods more highly than the others did. A larger proportion of this group listed mathematics-calculus and biostatistics-population dynamics as the most valuable subject, and social sciences and humanities-liberal arts as the least valuable. The proportion of them that recommended increased practice and experience in the curriculum was also greater.

The managers valued natural history and communications. A larger proportion of them rated ichthyology-systematics, ecology, fishery management, and public speaking as the most valuable subject. A smaller proportion of them than of the other two groups rated mathematics-calculus as the most valuable subject. A larger proportion of them also ranked biology, advanced chemistry, and physics as the least valuable course, but add aquacultural sciences, and recommended that courses have greater relevance to real life problems and that the curriculum include more communication skills.

The administrators valued general biology and wished they had taken more courses in the social sciences and administration. A larger proportion of them rated biology and invertebrate zoology-marine biology as the most valuable subject, wished they had taken more biology, social sciences, and administration, and recommended that the curriculum be improved by the addition of administration courses.

The teachers (although the sample was small) tended to be extreme in their opinion of several subjects. A larger proportion of them ranked the basic sciences—zoology, ecology, advanced zoology, chemistry, and oceanography-limnology—as the most valuable subject and a smaller proportion of them rated the applied biological sciences, the social sciences, and public speaking as the most valuable subject. Somewhat anomalously, a larger proportion of them recommend-

ed that the courses have greater relevance to real problems, emphasize more technical skills, more scientific methods, and be less specialized.

Type of Fishery

A preponderance of the fishery scientists work mostly with either recreational fisheries or commercial fisheries. Most of those working for the state fishery or fish and game agencies, the Bureau of Sport Fisheries and Wildlife, and the nonfishery agencies were concerned with recreational fisheries; and most of those working for the National Marine Fisheries Service and for universities were concerned with commercial fisheries. The balance included a few who divided their time equally between recreational and commercial fisheries and some who were extensively engaged in environmental problems.

The recreational fishery scientists valued natural history and environmental and communication subjects. A larger proportion of them than of the commercial fishery scientists rated ecology, ichthyology-systematic zoology, invertebrate zoology-marine biology, fishery management, oceanography-limnology, aquacultural science, and public speaking as their most valuable subject, wished they had added such subjects, and suggested that courses should have greater relevance to actual problems and the curriculum should have more environmental courses.

The commercial fishery scientists valued quantitative methods, fisheries, and economics. A larger proportion of them rated mathematics-calculus, fisheries-fishery biology, biostatistics-population dynamics-computer use, and economics as their most useful subject, wished they had added these subjects, and commented on the need to improve the curriculum by the addition of business and administration courses.

Fisheries vs. Biology-Zoology Major

More than 90% of the PFB respondents had majored in either fisheries, biology, or zoology. Those who had majored in fisheries frequently had minored in biology, zoology, or chemistry. Regardless of major, however, the distribution among duties and types of fisheries was almost the same.

A higher proportion of the fishery majors listed ichthyology-systematic zoology, mathematics-calculus, fisheries-fishery biology, fishery management, wildlife management, English composition, and public speaking as their most valuable subject, wished they had taken more ecology, ethology, psychology, and economics, and commented on the need for courses with greater relevance to real problems and on the need to add environmental courses.

On the other hand, a larger proportion of the biology-zoology majors listed ecology, physiology, and invertebrate zoology-marine biology as their most valuable subject, wished they had taken more calculus, geology-hydrology, and fishery management, and suggested less specialization in the curriculum.

Shifts in Opinions with Passage of Time

Information on the years since the last degree enabled a breakdown into three decade groups <10, 10-19, and >19 years with considerable numbers in each. Interpretation of the different opinions is difficult, however, because of changes in curricula, changes in status of the respondents with age, and dimmed memories.

The oldest group tended to cling to the traditional sciences and communications. A larger proportion of them rated biology, zoology, botany, chemistry, physics, English composition, and public speaking as the most valuable subject, wished they had had more of these subjects, and wished they had added more administration.

On the other hand, the youngest group valued more highly the environmental, quantitative, and applied sciences. A larger proportion of them rated ecology, ichthyology-systematic zoology, fishery management, and biostatistics-population dynamics as the most valuable subject. They also had stronger negative opinions; a larger proportion of them listed advanced zoology, chemistry, physics, economics, and humanities-liberal arts as the least valuable subject (although a slightly larger proportion of the intermediate age group rejected humanities-liberal arts).

COMPARISON OF OPINIONS FROM PFB AND FISH CULTURISTS

Few members of PFB were concerned with any kind of aquaculture; therefore a similar questionnaire was submitted to people in the western United States who were on a mailing list (December 1968) for the Northwest Fish Culturists Conference. The number of respondents was much smaller, perhaps because a considerable proportion of the fish hatchery superintendents lacked college degrees, but usable answers were obtained from 16 fish cultural supervisors and 19 fish cultural researchers. The first group included 7 without a baccalaureate degree, 9 with, and none with a higher degree. Of the second group all had baccalaureate degrees, 5 had master, and 7 doctorate degrees; 15 were employed by government laboratories.

A larger proportion of the fish cultural supervisors than of the PFB members rated physiology, oceanography-limnology, aquacultural sciences, and hydraulic engineering as the most useful courses. They found basic mathematics very useful but not higher mathematics or biostatistics-population dynamics, but many wanted to add courses in the latter. They listed English composition and public speaking as the most valuable course about as often as the PFB members did. Above all they wished they could have added more courses in the aquacultural sciences.

The fish cultural researchers valued subjects much differently from either the total PFB members or the PFB researchers. A larger proportion of them listed physiology, advanced biology, chemistry, advanced chemistry, physics, and the aquacultural sciences as their most valuable subject, and botany, sociology, and economics as their least valuable. Fewer of them than of the other two groups rated biostatistics-population dynamics as their most valuable subject but many wished they had taken more. Above all they wished they had taken more physiology, advanced chemistry, and aquacultural sciences.

COMPARISON OF OPINIONS FROM PFB AND STUDENTS

The questionnaire circulated to the PFB was also given to undergraduate and graduate seminar groups in the College of Fisheries of the University of Washington. Replies were received from 20 undergraduate and 28 graduate students.

There was a notable diversity of opinion among the undergraduates. A relatively large proportion listed the following subjects as the most valuable course and a similarly large proportion rated them as their least valuable: research methods, advanced chemistry, physics, fisheries-fishery biology, fishery management, and biostatistics-population dynamics. Because of this diversity, no critical comparison of their opinions with those of PFB members is possible; but they seemed to value zoology and communication courses much less than PFB members and aquacultural sciences more than PFB members.

The graduate students were much closer to PFB members in opinions and differed largely from them in only a few subject areas. A larger proportion of them rated physiology, biostatistics-population dynamics, and aquacultural sciences as the most valuable course, whereas fewer of them included chemistry and communications as the most valuable course. They differed especially with regard to communications; they had no understanding of its importance.

SUMMARY AND CONCLUSIONS

1. No single curriculum is ideal for training in fishery science. The field has become much too broad and includes too many specialties that each require a high level of training. The specialization is expected at graduate level, of course, but is desirable even at undergraduate level if students can anticipate either the graduate work or the type of job they will enter.

A corollary of the above conclusion is that a person with a terminal baccalaureate degree should not be a dropout from a research-oriented, two-degree or three-degree program. A majority of the jobs in fishery science has been held and probably will continue to be held by people with only a baccalaureate degree. Some of these jobs will be major administrative, decision-making jobs with rewards equal to those that will be open to holders of a doctorate degree.

2. A biology or zoology undergraduate major may be good preparation for graduate work in fisheries, but it is relatively poor preparation for a job. Advanced biology courses in general are much less useful than courses in English composition, public speaking, fishery science and management, and the quantitative sciences.

3. Student and faculty opinions about curricula are probably not the best guides. Both differ substantially from the opinions of a majority of the nonteaching professionals in the field, especially in their evaluation of subjects that develop the ability to deal with people.

4. Courses in the social sciences, humanities, and liberal arts have not been as useful as people now want them to be. With a few exceptions these subjects were characteristically among those listed as the least useful. The exceptions are important as indication of needed improvements because they include courses in resource economics and administration—both public and business. These are courses that are relevant to real problems, and it would appear that many social sciences-humanities-liberal arts courses have not been relevant hitherto.

5. The high value of general courses in science, both basic and applied, and the mixed value of advanced courses indicate the importance of teaching the general courses especially well.

6. There are advantages in a fishery education that is interrupted by periods of work. The student can form definite opinions about specialties that he needs for the job that he has or wants. In addition almost everyone can benefit from refresher courses that cover new developments.

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EFFECT OF CROWDING ON RELATION BETWEEN EXPLOITATION AND YIELD IN *TILAPIA MACROCEPHALA*

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ABSTRACT

An experiment was performed to assess the effect of crowding on yield in *Tilapia macrocephala*. Populations of nearly equal number and weight were started in control (155.2 liter) and test (77.6 liter) tanks. Food amounts and environmental attributes other than space were the same for both tanks. Each of the two populations was exploited—first at a bimonthly rate of 10% for 14 months, then at a bimonthly rate of 25% for 10 months.

Equilibrium yields at each rate for each tank (four points) were fitted with a Fox exponential surplus-yield model. Deviations from this general population curve showed that yields were greater for the larger tank at the 25% rate and greater for the smaller tank at the 10% rate. This is believed to result from the fact that the entire yield came from growth at the lower rate whereas part of the yield came from recruitment at the higher rate. A low rate of conversion of food to fish (18%) is believed to be due to the large proportion of liver in the diet.

Current interest in aquaculture suggests an imminent increase in the holding of fish in restricted enclosures. Such holding, particularly at high densities, provides the fish with a drastically altered environment as compared with their native habitat. Some of the effects are undesirable, as is only too well known to hatchery men. Metabolic wastes accumulate rapidly and some communicable diseases spread easily among enclosed populations. There may also be undesirable effects due to reduced area for spawning—for example, spawning fish that are close together may use more energy defending their territory against the intrusion of other fish than spawners that are farther apart. Effects of crowding can also be beneficial, such as increased growth rate with less expenditure of energy in swimming.

The purpose of the experiment described here was to investigate one class of results from crowding—those related to the yield in self-sustaining populations. Of many possible experimental animals, *Tilapia macrocephala* belongs to a genus which is already important in pond culture. This species is small enough to raise in laboratory tanks and has reasonably rapid reproduction and growth. A conventional control-test design was adopted in which the control population was in a tank that had been demonstrated as being of suitable size for *T. macrocephala*. The test population was in a tank exactly one-half the size of the control tank. Food, light, temperature, and initial populations were kept as nearly identical as possible.

MATERIALS AND METHODS

Two conventional glass-wall aquarium tanks were used. The water mass in the control (larger) tank (L) had a volume of 155.2 liters, with approximate dimensions 39 by 90 by 44 cm. Volume of the test (smaller) tank (S) was one-half that of L, or 77.6 liters. To keep proportions the same, linear dimensions of S and its equipment were $1/2^{1/3}$ those of L.

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Tank L was provided with two fiber-charcoal filters, each with an electric pump delivering 2,800 ml per min; tank S had one of these.

Aeration was by one airstone in tank L and two in tank S.[3] Oxygen concentrations varied from 4.4 to 7.4 ppm for L and 2.4 to 7.2 ppm for S.

Illumination was by overhead pink fluorescent lamps, which screened out violet-blue light, found by Perlmutter and White (1962) to be lethal to some fish eggs. Lights were controlled by an automatic switch, turned on from 6 AM to 6 PM each day.

Each tank had shelter in the form of cords suspended from plastic floats. Forty-four cords 30 cm long were attached to a 49- by 15-cm float in tank L; numbers and dimensions of the shelter were proportional in tank S. A floating fiber brush type shelter, 4 cm in diameter by 25 cm long, was in L, and a proportional one was in S. The back, one side, and part of the front of each tank were rendered opaque with black plastic; the front area was 44 by 20 cm in L and proportional in S.

Refuges for young fish were enclosed at the end of each tank by fences consisting of 5-mm diameter plastic rods spaced 3 mm apart. The enclosed area was 14 cm wide in L and proportional in S. Aquarium gravel was placed in the bottom of each tank for nesting activity.

Both tanks were maintained at room temperature, which was thermostatically controlled except that cooling was not available in the summer. Weekly mean temperatures were 24 ± 2°C for both tanks.

Fish were fed daily according to a fixed schedule (Table 1). Uneaten food, feces, and other detritus were siphoned out daily, and two-thirds of the water mass was changed each week, using tap water brought to tank temperature. Charcoal and fiber in the filters were changed once weekly.

Populations were counted and weighed every 2 months. Since *T. macrocephala* is a mouth breeder, it was not desirable to handle the fish more often. Aronson (1949) stated that the mean spawning interval for the species was 15 days, so the counting interval was about four brood intervals. Exploitation was performed at the time of counting by removing the tenth or fourth fish for 10% and 25% exploitation rates. Weighing was done by draining fish in a net, placing them in a weighed container with water, weighing the container with fish, and subtracting the tare.

TABLE 1.—Amounts (grams) of food placed in each tank.

Day of week	Trout pellets		Tropical fish food	Liver	Total
	Moist	Dry			
Sunday	6.0	1.5	1.5	--	9.0
Monday	1.5	1.5	0.9	9.0	12.9
Tuesday	1.5	1.5	0.9	9.0	12.9
Wednesday	1.5	1.5	0.9	9.0	12.9
Thursday	1.5	1.5	0.9	9.0	12.9
Friday	1.5	1.5	0.9	9.0	12.9
Saturday	1.5	1.5	0.9	9.0	12.9
Total	15.0	10.5	6.9	54.0	86.4

Exploitation started in December 1967, with 42 fish weighing 1,148 g in S and 45 fish weighing 1,167 g in L (Table 2). These fish were either survivors or descendants of a shipment of 10 adults and 50 young fish received on 10 February 1966 by air from the Honolulu Biological Laboratory of the Bureau of Commercial Fisheries (now National Marine Fisheries Service).

Although numbers of fish declined at the 10% bimonthly exploitation rate (Figure 1), biomass remained relatively constant (Figure 2) and no evidence of recruitment was observed. To determine if recruitment would occur at a lower biomass, the exploitation rate was increased to 25% at month 16 and was continued at that rate until the end of the experiment. It will be shown below that recruitment did occur under the higher exploitation rate.

RESULTS

VITAL PROCESSES

Significant results from exploitation experiments require that recruitment and growth occur during the course of the experiment. It is also desirable to know whether natural (nonfishing) mortality was occurring. Evidence relating to these vital processes can be obtained by exam-

[3] Although these numbers may appear to be reversed, they are as used. The oxygen concentrations show that they provided approximately equal aeration.

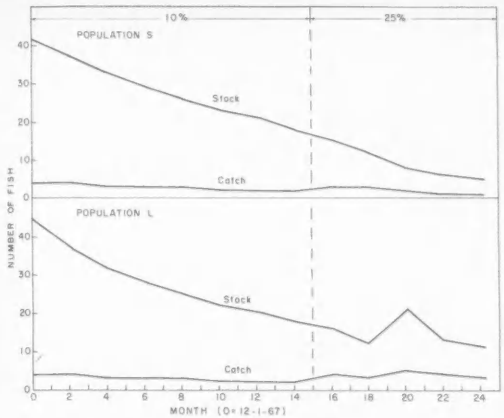

FIGURE 1.—Bimonthly stocks and catches, numbers, *Tilapia macrocephala*, 77.6-liter (S) and 155.2-liter (L) tanks. Percentages indicate target bimonthly exploitation rates.

ining net changes in number (R_{INT}) during the intervals between counts (Table 3).

Recruitment is defined here as survival of young fish to the size that could not pass through the 3-mm openings of the refuge fence. On this basis, no recruitment was apparent during the period of 10% exploitation, months 0-14 (Table 3). However, it is possible that some did occur, balanced by unrecorded mortality. Deaths not recorded are indicated by negative values of R_{INT} (Table 3). Also, it is almost certain that spawning occurred in which the resulting young were victims of cannibalism before reaching recruit size. Positive values of R_{INT} after month 14 show that recruitment occurred in both S and L under the 25% exploitation rate, with recruitment in L about double that in S.

Growth of individual fish can be detected by observing concurrent changes in numbers and biomass. Growth was demonstrated from month 0 to month 12.3, when biomass increased and numbers decreased in both S and L (Table 2, Figures 1 and 2).

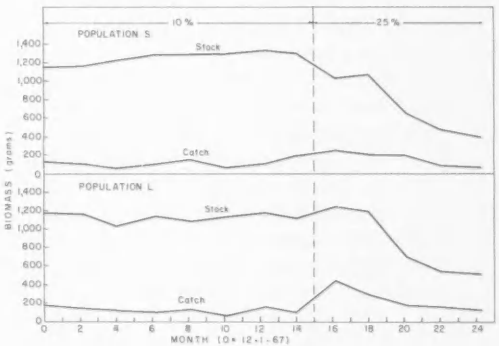

FIGURE 2.—Bimonthly stocks and catches, weights, *Tilapia macrocephala*, 77.6-liter (S) and 155.2-liter (L) tanks. Percentages indicate target bimonthly exploitation rates.

TABLE 2.—Population[1] and catch, *Tilapia macrocephala*, in two sizes of tanks during bimonthly exploitation.

Target exploitation rate[2]	Month[3]	S—77.6-liter tank				L—155.2-liter tank			
		Number		Weight (g)		Number		Weight (g)	
		Stock	Catch	Stock	Catch	Stock	Catch	Stock	Catch
0.10	0.0	42	4	1,148	132	45	4	1,167	178
	2.2	37	4	1,159	103	37	4	1,159	143
	4.0	33	3	1,216	47	32	3	1,026	122
	6.2	29	3	1,293	100	28	3	1,142	104
	8.1	26	3	1,288	153	25	3	1,076	126
	10.1	23	2	1,299	63	22	2	1,137	62
	12.3	21	2	1,338	109	20	2	1,181	160
	14.0	18	2	1,308	205	18	2	1,120	101
0.25	16.2	15	3	1,028	262	16	4	1,246	450
	18.0	12	3	1,080	216	12	3	1,195	297
	20.1	8	2	676	211	21	5	725	183
	22.0	6	1	496	102	13	4	562	156
	24.3	5	1	419	81	11	3	529	134

[1] In the 77.6 liter tank the population was replaced after accidental mortality at month 19. Also, sex ratio was changed from 1 male:5 females to 3 males:3 females at month 21.2.
[2] Because of the relatively small numbers of fish, the effective exploitation rates varied considerably from these. In fitting the population model, the effective rates in terms of weight were used.
[3] 0 = December 1, 1967.

Both recorded and unrecorded natural mortalities occurred. Recorded mortality represented finding of dead fish in the tanks. Unrecorded mortality, as mentioned above, is demonstrated by negative values of R_{INT} (Table 3).

TABLE 3.—Recruitment and unrecorded mortality, *Tilapia macrocephala*. $R_{INT} = P_{n+1} - P_n + M_{INT} + C_{INT}$, where INT is interval between counts n and $n+1$, R is net change,[1] P is stock, M is recorded mortality, and C is catch, all in numbers.

Interval (months)	R_{INT} for:	
	Population S—77.6-liter tank	Population L—155.2-liter tank
0- 2.2	−1	−2
2.2- 4.0	0	−1
4.0- 6.2	−1	0
6.2- 8.1	0	0
8.1-10.1	0	0
10.1-12.3	0	0
12.3-14.0	−1	0
14.0-16.2	+1	0
16.2-18.0	0	0
18.0-20.1	+4	+12
20.1-22.0	0	−2
22.0-24.3	+3	+3

[1] $R_{INT} > 0$ indicates recruitment of at least the indicated number of fish, $R_{INT} < 0$ indicates unrecorded mortality of at least the indicated number, and $R_{INT} = 0$ indicates either no recruitment and unrecorded mortality, or the two exactly balanced.

CHANGES UNDER EXPLOITATION

Responses of the populations varied with exploitation rate. At the 10% rate, numbers in each population declined while biomass remained relatively constant (Figures 1 and 2). At the 25% rate, both numbers and weights declined. Further consideration of stock changes will be limited to data of biomass, since the biomass curves are more regular than those of numbers and represent both recruitment and growth. It is evident that the initial rise in weight of catch at the 25% rate was due almost entirely to cropping off the biomass accumulated at the 10% rate (Figure 2). The response of both populations to an increase in exploitation rate thus followed classical conceptions based on theoretical grounds (for instance, those of Thompson and Bell, 1934).

EQUILIBRIUM YIELDS

In a relatively short experiment, such as this, covering only 13 exploitation periods, the attainment of complete equilibrium at either of the exploitation rates is obviously impossible. The last two exploitation periods at each rate encompass relatively small changes in stock and catch (Figure 2); they will thus be considered equilibrium periods for the purposes of the analyses reported below.

POPULATION MODEL

The exponential surplus-yield model of Fox (1970) is simple to fit and has been found suitable for experimental populations with short brood intervals (Silliman, 1971); it was therefore chosen for use with the data from the *T. macrocephala* experiment. Ideally, the model would be fitted to S and L separately. The regression method employed for fitting does not perform well when only two points are available. There is no opportunity for compensating errors, and slight errors are greatly magnified when the regression is extrapolated to the Y-intercept to estimate the maximum stock. Also, since there are zero degrees of freedom, there is no way of assessing variability.

The above difficulties can be circumvented by fitting a single general curve to both populations. For individual population characteristics, deviations from the general curve can be studied. Four points were available for fitting the regression line—two from each population (Figure 3). The fit seems reasonably good for an experiment of this type.

COMPARISON OF YIELDS

Deviations from the general curve (Figure 3) may be considered with respect to the crowding effect. It is seen that at the lower exploitation rate (10% target) and larger population, the population in the smaller tank (S) has a large positive deviation whereas that in the larger tank (L) is close to the curve. Conversely, at the higher exploitation date (25% target) and

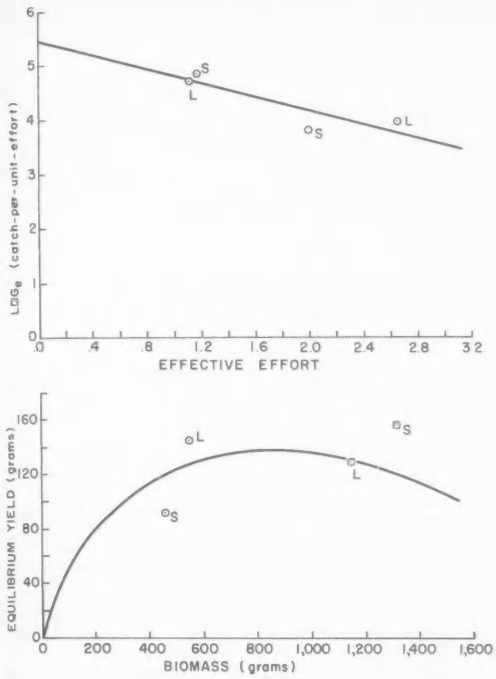

FIGURE 3.—Effort-CPUE line (least squares fit) and biomass-yield curve, fitting of Fox (1970) model. CPUE assumed proportional to population size. L indicates population in 155.2-liter tank and S in 77.6-liter tank.

smaller population, L has a positive deviation and S a negative.

An explanation for this seemingly paradoxical finding may be found in the source of the yield at each exploitation rate. At the lower rate, during months 0-14, the populations were large and no recruitment occurred (Figure 2, Table 3). The yield that did occur, then, resulted entirely from growth. Under the higher exploitation rate prevailing during months 16-24.3, the population was smaller and recruitment did occur (Figure 2, Table 3), furnishing part of the yield. Growth could have been retarded in the larger tank by greater expenditure of energy in swimming. Recruitment could have been favored in that tank by psychological factors controlling spawning, by greater opportunity for newly released young to escape cannibalism, or by a combination of these factors.

The finding of greater growth in the smaller tank is in contradiction to the conclusions of Chen and Prowse (1964) for *T. mossambica*. Examination of their data, however, shows that these conclusions were based on results from their largest ponds (0.10-0.40 ha) after a year of growth. Data comparing their smaller ponds were available only to 6-months' growth and are less clear cut. For instance, at 6 months their 0.04-ha pond showed greater growth than their 0.20-ha pond. Even their smallest pond (0.004 ha and 76 cm depth) had a volume of 31,000 liters, or 200 times that of the larger tank in the *T. macrocephala* experiments. With a different species (even though in the same genus) and such a vast difference in size of habitat it is perhaps not surprising that their findings are at variance with those reported here.

In both the present experiment and that of Chen and Prowse, the term "crowding" can be used only in a relative sense and not in the sense of lack of space to move about. Assuming the fish have the same density as water (nearly true), the maximum population in the smaller tank of the present experiment occupied only 1.72% of the water. The maximum concentration in Chen and Prowse's experiments was 0.02%. Thus, whatever effects occur must result from such factors as relative distance swum or sociological phenomena, like aggression. Chen and Prowse chose the latter, although it is a bit difficult to imagine when there are 2 or less kg of fish per 10,000 liters of water.

Finally, yields may be compared as measures of conversion[3] of food to fish flesh. The maximum bimonthly sustainable yield from the general population curve (Figure 3) is about 140 g (calculated value, 137.8 g). Food provided during each 2-month period weighed 749 g (8⅔ weeks × 86.4 g weekly total fed, as shown in Table 1). Apparent conversion was thus 18%.

The above results may be compared with those from the growth experiments of Swingle (1960)

[3] Used here in the sense of net growth in weight (= sustainable yield) expressed as a percentage of weight of food made available to the population.

in 0.40-ha ponds. His data are not directly comparable, however, as he fertilized the ponds in addition to feeding the fish. A rough correction may be made by subtracting growth achieved in unfed groups of fish. By doing so, a mean of 42% is obtained for *T. mossambica* in seven experiments starting with brood stock and lasting a single growing season. The much poorer showing of *T. macrocephala* in the present experiment is believed to be partly due to the large proportion of liver included in the diet (Table 1). Substantial amounts of uneaten liver were often removed from the tanks during daily cleaning. Also, the population density in Swingle's ponds was about two orders of magnitude less than in the present experiment, which may bear on the difference in food conversion. His ponds were about the size of the larger ones used by Chen and Prowse (1964), so their finding of greater growth in larger ponds may account for some of the superiority in growth found by Swingle.

ACKNOWLEDGMENTS

My thanks are due to Dr. Ralph Hile for suggesting an experiment to study space effects. Initial stocks were contributed by the National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory through the kindness of Heeny S. H. Yuen and Robert T. B. Iversen. George F. Slusser developed the diets and experimental procedures. The populations were maintained by Martin G. Beam, Jimmy R. Chrnaoski, and Judy A. Trauth.

As part of the O. E. Sette dedicatory volume, I gratefully dedicate this small contribution to him. He was my first research supervisor (1938-45), and I owe a very great deal indeed to his encouragement, advice, and instruction during those formative years of my career.

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VARIATIONS IN SIZE AND LENGTH COMPOSITION OF ATLANTIC MENHADEN GROUPINGS

FRED C. JUNE[1]

ABSTRACT

This paper gives estimates of size (weight) and length composition of summer schools and fall school-aggregations of Atlantic menhaden based on single-set purse-seine catches and accompanying catch samples obtained in 1955-62. The data show that the fish school by length and the average size of summer schools decreases as the apparent abundance of fish in a given area of the coast decreases. The significance of the school concept in the study of the dynamics of the population and the effects of fishing upon it are discussed, and additional avenues of research are suggested.

The Atlantic menhaden, *Brevoortia tyrannus*, is a schooling fish that occurs in the western Atlantic Ocean from Nova Scotia to Florida and is the object of a purse-seine fishery over most of its range (Reintjes, 1969). The fishery is based on seasonal appearances of the fish schools in shallow waters overlying the inner half of the continental shelf (Roithmayr, 1963). Fishermen and aerial fish spotters, who locate and assist in the capture of menhaden, have a working knowledge of school size, composition, and behavior, but there exists little quantitative information on these and other aspects of the schooling phenomenon. Of primary interest to the fishery biologist are the degree to which the fish school by size, the relationship between size of schools and size of fish within schools, and the variation in size of schools in relation to changes in abundance of the fish and to fishing. These aspects of Atlantic menhaden schooling are the subject of this paper.

The nature of density and fishery-related changes in the schooling of various pelagic marine fishes is not well understood, but sufficient evidence was put forward by different workers to indicate insight into the importance of this behavioral phenomenon. The significance of the school concept in the study of the dynamics of an exploited fish population whose members are grouped and differentially distributed by size was apparently first recognized by Thompson (1926) and further elaborated by Sette (1943) for the Pacific sardine (*Sardinops sagax*). Much of the quantitative information on fish schooling dynamics has come from work on tunas. Schaefer (1948) and Brock (1954), for example, discussed some implications of observed variations in the size of fish within and between schools in the design of a sampling system for yellowfin (*Thunnus albacares*) and skipjack (*Euthynnus pelamis*) tuna stocks, respectively. Orange, Schaefer, and Larmie (1957) and Broadhead and Orange (1960) offered evidence of fishery-related changes in the schooling dynamics of yellowfin tuna, while Brock (1962) considered implications of the interrelationship between the size and number of yellowfin tuna forming a school and the success of longline fishing. June and Reintjes (1959) established that the Atlantic menhaden also schools by size, and they concluded that the school is therefore the appropriate unit for sampling the size, age, and sex composition of the population. They further demonstrated seasonal and annual variations in the estimated number and geographical distribution of purse-seine sets on menhaden schools in a series of reports beginning with 1955 (June and Reintjes, 1959), and Roithmayr (1963)

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summarized these data for the years 1955-59. There has been no further elucidation of the schooling dynamics of this fish. This study pursues that objective.

SOURCES AND TREATMENT OF DATA

The basic data consisted of fishing logbooks maintained aboard menhaden vessels for use by the National Marine Fisheries Service and reduction plant records of daily vessel landings from 1955 to 1962. Of the single-set catches recorded in the logbooks, only those for which the "hailed" catch was within 10% of the plant weights were used in the analyses. Vessel landings at the reduction plants were converted to metric tons.

I assumed that each purse-seine set during the "summer fishery" (April-September) was made on a discrete school of Atlantic menhaden. Sets made on large aggregations of fish that appeared off Long Island in late September or early October (June and Nicholson, 1964) and off North Carolina in November and December were considered separately.

Despite the rigorous screening of fishing logbooks, several sources of error may have been involved in the identification of single-school catches and estimates of school size. Foremost of these are (1) a portion of a school may have escaped during capture, (2) a variable loss in weight from decomposition may have occurred within single-school catches of the same initial size (such losses would be proportionately greater during warmer weather and in catches made at the beginning of the fishing day), and (3) a single recorded set may have actually included more than one set. Items (1) and (3) would have a greater effect on the catch estimates, but there is no way of determining the extent of these sources of error in this study; item (2) must be considered a random factor.

Catch samples, which provided measures of fish size, were taken from daily vessel landings at reduction plants along the Atlantic coast (Figure 1) as part of a routine catch-sampling program begun in 1955 (June and Reintjes, 1959). Fish lengths were grouped in ½-cm classes. The mean length, variance, and standard deviation and the mean weight, in grams, of fish in each catch sample were computed.

The number of fish within a single-set catch was determined by dividing the weight of the catch by the mean weight of the fish in the catch sample. A catch sample was obtained from 275 single-school catches during the summer fishery and from an additional 64 single-set catches from the large fall aggregations of fish off Long Island (23 sets) and North Carolina (41 sets).

Detailed logbook information and accompanying plant weights were available for 2,643 single-school summer catches and an additional 286 single-set fall catches off Long Island (138 sets) and North Carolina (248 sets). The number of single-school summer catches for which there were data constituted about 1% of an estimated 240,000 purse-seine sets made during the 8 seasons. Except for 1961 and 1962, when a combined total of only four single-school summer catches were recorded for the South Atlantic Area, single-set catches were taken throughout the range and period of fishing and are therefore believed to be representative of the schools or larger aggregations of fish into which the population was divided.

SEASONAL GROUPINGS OF THE FISH

Examination of 2,643 single-school summer catches indicated wide variation in school size (weight). A plot of the combined frequencies of single-school catches for the 8 seasons, by 3-ton size classes (upper panel, Figure 2), shows a pronounced skewness in the distribution toward smaller catches, with the mode occurring in the 4- to 6-ton size class. Single-school catches ranged from 0.3 to 103 tons. The grand mean for the 8 seasons was 16.6 tons, with a standard deviation of 12.25 tons. The size-frequency distributions of single-school catches in individual seasons (lower panels, Figure 2) also were asymmetrical and, without exception, similar in shape to that of the combined data. The maximum frequency in every year fell in either the 4- to 6-ton or the 7- to 9-ton size classes.

Although there were exceptions in some years, larger schools were generally found in the north-

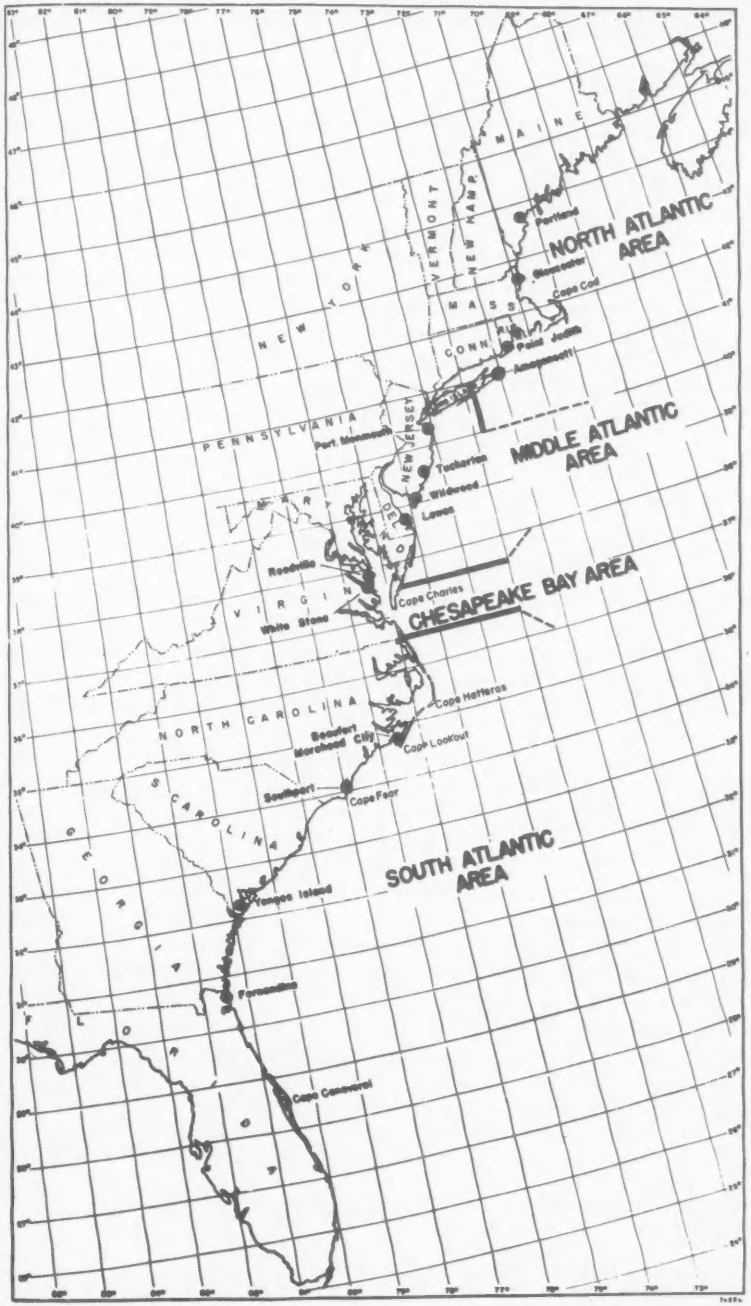

FIGURE 1.—Locations of reduction plants where Atlantic menhaden catch samples were collected and the four major geographical areas used in summarizing the biostatistical data.

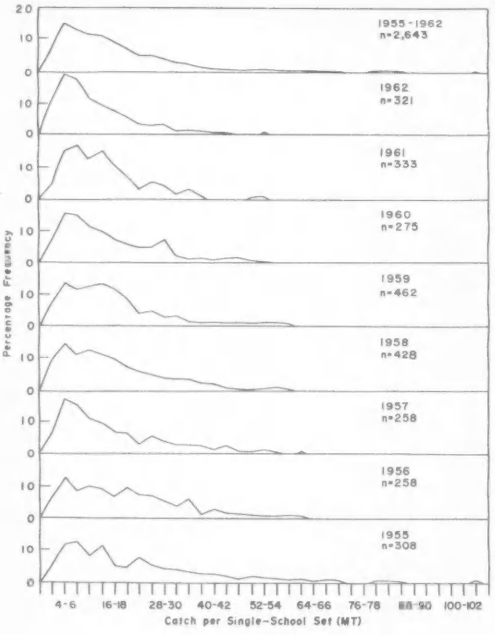

FIGURE 2.—Percentage size-frequency distributions of 2,643 single-school summer purse-seine catches of Atlantic menhaden, 1955-62.

ern part of the range during the summer, and progressively smaller schools occurred at lower latitudes. Comparison of the mean catch per single-school set within the four major areas of the summer fishery (Table 1) shows that schools in the North Atlantic Area averaged about 21 tons per set and 5 to 9 tons heavier than those in other areas. Schools in the Middle Atlantic Area were intermediate in size, averaging about 16 tons per set, while those in the Chesapeake Bay and South Atlantic Areas were smallest, averaging about 13 tons per set.

Size of summer schools declined from 1955 to 1962. The mean catch per single-school set in 1955 was 22 tons; it decreased and fluctuated around 16 tons from 1957 to 1960, and in 1962 it was only about half that in 1955 (Table 1). This decline was largely attributable to a reduction of school size in the North Atlantic and Middle Atlantic Areas, where decreases in the means amounted to about 40% over the 8-year period. In general, mean school size in the Chesapeake Bay and South Atlantic Areas fluctuated only slightly about their grand means. The high mean for Chesapeake Bay in 1955 resulted from several large single-school catches recorded at the beginning of the fishing season and probably is atypical (see also p. 704). Too few single-school catches were recorded in the South Atlantic Area in 1961 and 1962 (1 and 3, respectively) to be considered in calculation of these seasonal means. But in view of the relatively small size of single-school summer catches in previous years, additional data from this area in 1961 and 1962 would likely not have influenced the grand seasonal means.

There was a definite change in the grouping of the fish in autumn. In every year schools became noticeably reduced in number in surface waters of the Gulf of Maine in late August or early September, and during late September or early October large masses of fish, or "school aggregations,"[2] appeared off Long Island, only to disappear from these waters by mid or late

[2] To avoid confusion, the word aggregation is used in this paper in its general meaning and not as defined by Breder (1959).

TABLE 1.—Mean size of single-school summer catches of Atlantic menhaden from 2,643 purse-seine sets in the four major statistical areas, 1955-62. The number of sets used in calculating the means are given in parentheses.

Area	Year								Grand areal mean	Standard deviation
	1955	1956	1957	1958	1959	1960	1961	1962		
	metric tons									
North Atlantic	25.9(91)	26.4(75)	22.2(58)	18.8(78)	23.3(88)	19.2(80)	18.6(87)	15.8(48)	21.1(605)	15.32
Middle Atlantic	22.0(177)	17.3(154)	16.4(163)	16.7(258)	15.1(266)	15.4(163)	13.5(227)	13.2(163)	16.1(1,571)	11.72
Chesapeake Bay	21.9(19)	12.3(13)	11.0(19)	15.3(64)	12.4(28)	10.7(14)	12.0(19)	10.5(110)	12.8(286)	8.59
South Atlantic	11.5(21)	14.3(16)	10.3(18)	13.6(28)	12.5(80)	14.0(18)	---	---	12.6(181)	7.15
Grand seasonal mean	22.4(308)	19.5(258)	16.9(258)	16.7(428)	16.1(462)	16.2(275)	14.8(333)	12.7(321)	16.6(2,643)	12.25

October (Roithmayr, 1963; June and Nicholson, 1964; Nicholson, 1971a).

Single-set catches from fall school-aggregations, on the average, were larger than single-school summer catches. A plot, by 3-ton size classes, of 138 single-set catches made from large fall school-aggregations that appeared off Long Island shows a marked difference in the shape of the frequency polygon when compared with that of single-school summer catches in the North Atlantic Area (lower and middle panels, Figure 3). The ranges of the two distributions are nearly identical (3 to 102 metric tons for the fall school-aggregations), but the curve representing fall school-aggregations is more symmetrical and its mode considerably higher (40- to 42-ton size class) and in much closer agreement with the mean of the distribution (44.4 metric tons). Moreover, single-set catches from fall school-aggregations, on the average, were over twice as large, and the standard deviation of their frequency distribution was 1½ times greater than that of single-school summer catches in the North Atlantic Area (Table 2). Comparisons within years show the mean catch from fall school-aggregations to be from 1½ to 3½ times larger than the mean single-school summer catch in the North Atlantic Area.

Differentiation of summer schools and fall school-aggregations was also indicated by the fact that the mean single-school summer catch in the North Atlantic Area decreased over the 8-year period, whereas the mean single-set catch from the fall school-aggregations off Long Island generally increased (cf. Tables 1 and 2). Although the two seasonal catches were negatively correlated ($r = -0.228$), the coefficient has no statistical significance.

Following the disappearance of the fish from coastal waters of southern Long Island and elsewhere in October, large school-aggregations reappeared off the coast of North Carolina in November of every year. These aggregations were usually first intercepted by the fishing fleet in the vicinity of Cape Hatteras, N.C., and fished as they moved southwestward along the coast until they disappeared off Cape Fear, N.C., in December or early January (Roithmayr, 1963; Nicholson, 1971b).

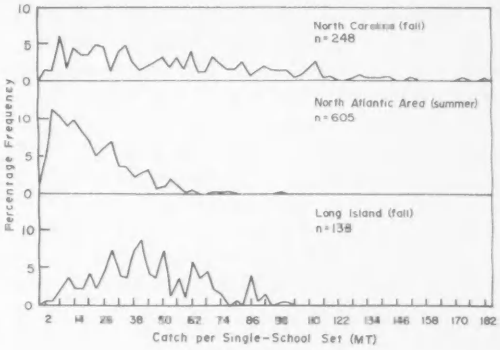

FIGURE 3.—Percentage size-frequency distributions of 138 single-set purse-seine catches of Atlantic menhaden from fall school-aggregations off Long Island (lower panel), 605 single-school summer catches in the North Atlantic Area (middle panel), and 248 single-set catches from fall school-aggregations off North Carolina (upper panel), 1955-62.

Single-set catches from fall school-aggregations off North Carolina, on the average, were the largest recorded along the Atlantic coast. A plot of 248 catches (upper panel, Figure 3) shows a range of 1.5 to 180 tons. The grand mean for the 8-year period was 54.2 tons, with a standard deviation of 37.63 tons. Thus, these catches, on the average, were from three to nearly five times heavier than single-school summer

TABLE 2.—Mean size of catches of Atlantic menhaden from 138 purse-seine sets on fall school-aggregations off Long Island and 248 sets on fall school-aggregations off North Carolina, 1955-62. The number of sets used in calculating the means are given in parentheses.

Locality	Year								Grand mean	Standard deviation
	1955	1956	1957	1958	1959	1960	1961	1962		
	metric tons									
Long Island	42.3(21)	37.8(12)	39.3(16)	34.1(10)	52.2(14)	47.3(26)	39.7(18)	54.3(21)	44.4(138)	21.77
North Carolina	34.8(29)	58.0(16)	46.1(43)	44.0(22)	58.6(32)	42.2(19)	69.7(72)	57.8(15)	54.2(248)	37.63

catches in the South Atlantic Area and were most similar in size to catches made 1 to 3 months earlier from school-aggregations off Long Island (Table 2).

In summary, the data presented demonstrate heterogeneity in the seasonal and areal grouping of Atlantic menhaden. Two basic groupings are evident: (1) summer schools, which are variable in size, comprised of discrete and independent clusters of fish, and differentially distributed over the range of the species, and (2) fall school-aggregations, which are large, but of undetermined size, and found only along their apparent southward migration route.

Questions immediately arise concerning the grouping of the fish following their disappearance off North Carolina through the time of their return northward migration in early spring. During this roughly 3-month period they are usually not seen at the surface. The spring movement seems to be largely over by the time that summer schools reappear in the inshore surface waters and become available to the purse-seine fishery. Inspection of first-of-the-season single-school catches suggested that some of these were larger than those taken immediately afterward, but the numbers of such catches were too few in most years to test this hypothesis statistically. Table 3, for example, gives available data on single-school catches during the first week of fishing in each major area (cf. Table 1). A plot of school size on time, however, indicated no clear relationship and in most years was similar to that shown in Figure 4. Thus, elucidation of the off-fishing season grouping of the fish awaits further study.

LENGTH OF FISH WITHIN AND BETWEEN GROUPINGS

There was a tendency for fish within summer schools to be of similar lengths, although the difference between the largest and smallest indi-

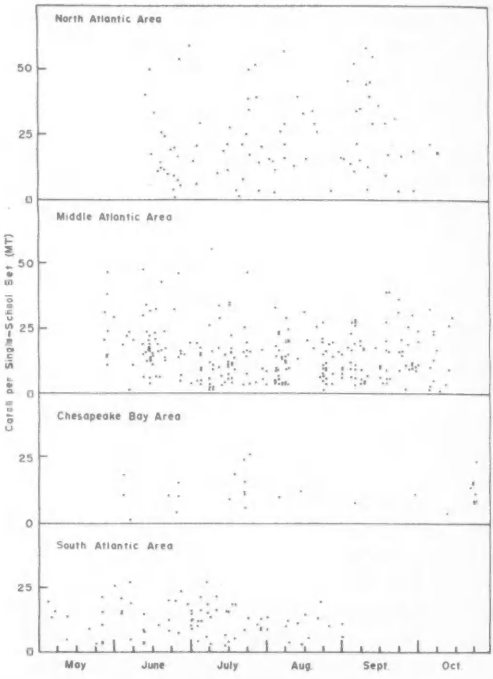

FIGURE 4.—Size of 462 single-school summer purse-seine catches of Atlantic menhaden in the four major statistical areas in 1959 plotted against time.

TABLE 3.—Size of single-school purse-seine catches of Atlantic menhaden made during the first week of the fishing season in the four major statistical areas, 1955-62.

Year	Area											
	North Atlantic			Middle Atlantic			Chesapeake Bay			South Atlantic		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
		metric tons			*metric tons*			*metric tons*			*metric tons*	
1955	6	11-63	37.7	32	4-72	35.4	3	20-43	30.7	–	--	--
1956	6	7-49	29.2	12	3-47	19.6	4	4-35	17.8	–	--	--
1957	–	--	--	13	2-33	11.8	1	--	8.0	3	8-21	12.7
1958	2	12-32	21.7	3	10-23	16.0	–	--	--	–	--	--
1959	4	18-49	35.4	15	2-47	22.0	2	11-18	14.6	5	5-19	13.3
1960	3	17-41	29.4	3	10-34	23.9	–	--	--	–	--	--
1961	6	8-28	17.2	16	5-28	15.9	1	--	13.3	–	--	--
1962	3	7-30	17.5	14	7-57	23.0	3	10-29	22.8	–	--	--

viduals within a school was variable. The mean of the length range of fish within samples from 275 single-school summer catches was 5.8 cm, with a standard deviation of 2.11 cm; the range was 1.5 to 13.0 cm. The seasonal means ranged from 5.1 to 6.8 cm, with no trend indicated during the 8 years. These findings support Breder's (1959) generalization that the difference in size of fish that will form an acceptable school does not exceed 50%.

To determine if variations in the length range within summer schools were associated with the relative lengths of the members, I plotted the variance against the mean length of fish in samples from 275 single-school catches (Figure 5). The variances obviously are heterogeneous, with variation within schools being greater among fish that averaged over about 25 cm in length.

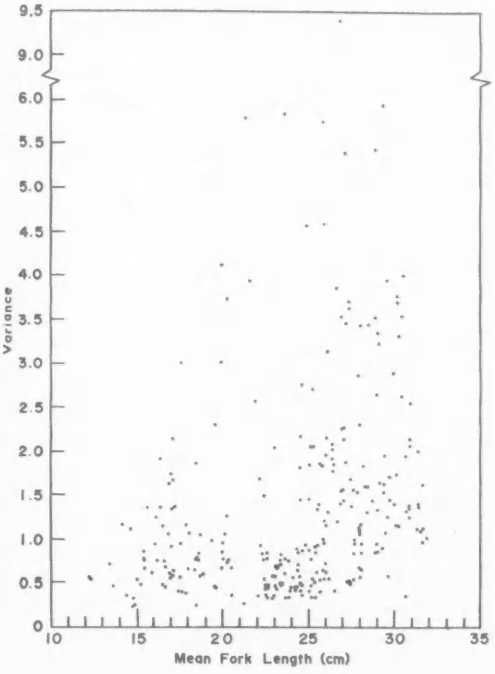

FIGURE 5.—Variance plotted against the mean of the length-frequency distribution of Atlantic menhaden in samples from 275 single-school summer purse-seine catches, 1955-62.

A plot of variances on time failed to show any trend within or between seasons. Thus, while summer schools of Atlantic menhaden are highly length-selective, schools of mixed lengths do occur, and variation seems to be greater within schools of larger fish than within schools of smaller fish.

The length range of fish within individual summer schools was less than the length range among schools inhabiting any given area of the coast, or of the population as a whole. In Figure 6, for example, are graphed the length-frequency distributions of fish in samples from 52 single-school catches made throughout the range of the summer purse-seine fishery in 1959. The least range in length within schools was 3.0 cm and the greatest 12.0 cm; the mean difference was 6.1 cm, with a standard deviation of 2.42 cm. In general, these data show that the lengths of fish found in the different areas of the coast varied considerably, and there was a decrease in

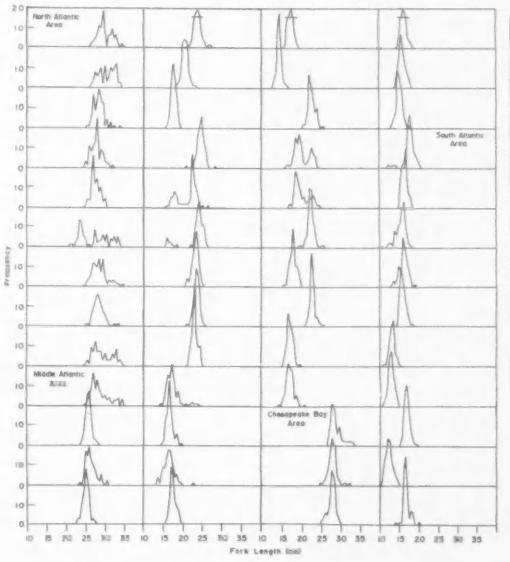

FIGURE 6.—Length-frequency distributions of Atlantic menhaden in samples from 52 single-school summer purse-seine catches in 1959. The samples are grouped by major statistical areas and arranged in order of decreasing latitude.

length with a decrease in latitude. But the important features of interest are the unimodality of most of the distributions, the decrease in variability within schools as the fish get smaller, and the comparatively narrow range of fish length within schools in contrast to the wide range of fish length within each area as a whole (cf. Nicholson and Higham, 1964). In the Middle Atlantic Area, for example, the length range within single-school catch samples varied from 3.0 to 10.1 cm, whereas the length range for the combined single-school catches sampled in that area was 21.5 cm (13.0 to 34.5 cm). So the segment of the population inhabiting any given area of the coast during the summer is evidently stratified, with each stratum comprised of discrete schools of fish grouped according to length.

Fall school-aggregations off Long Island consisted of large fish that were only represented in the North Atlantic Area during the summer. Length-frequency distributions of fish in samples from 23 single-set catches from these school-aggregations tended to be unimodal and contained relatively few fish under 25 cm (Figure 7). The range in length of fish within individual catch samples varied from 4.0 (28.0 to 32.0 cm) to 11.0 cm (23.0 to 34.0 cm). The mean length range within samples (7.3 cm, with a standard deviation of 1.81 cm) was slightly greater than that within samples from single-school summer catches in the North Atlantic Area (6.6 cm, with a standard deviation of 2.02 cm), but the difference between the means has no statistical significance.

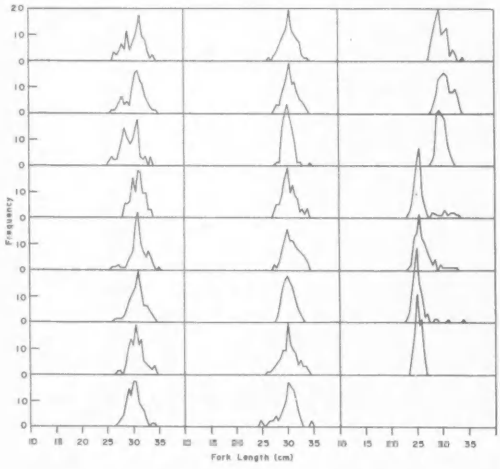

FIGURE 7.—Length-frequency distributions of Atlantic menhaden in samples from 23 single-set purse-seine catches from fall school-aggregations off Long Island, 1955-62.

The fall migratory school-aggregations off North Carolina consisted of length-groups represented farther northward during the summer, and individual aggregations contained fish of similar lengths. Fish lengths represented in samples from 41 single-set catches from these school-aggregations ranged from 8.5 to 35.0 cm (Figure 8). Because of selective fishing by the fleet on school-aggregations comprised of larger fish, the catch samples are accordingly weighted. The smallest length groups include young-of-the-year fish which had emigrated from estuarine nurseries at the end of the summer (June and Nicholson, 1964; Kroger, Dryfoos, and Huntsman, 1971). The most striking feature of the length-frequency curves is the relative homogeneity of fish lengths within individual school-aggregations, i.e., small fish are not represented in catch samples containing large fish, or vice versa. The least range in length within samples was 4.0 cm (9.0 to 13.0 cm) and the greatest 12.0 cm (22.0 to 34.0 and 22.5 to 34.5 cm). The mean of the range in length within samples was 8.4 cm, with a standard deviation of 6.13 cm. This was the largest mean difference and the greatest variation about the mean for any group of samples examined in this study. The length-frequency distributions of fish over about 25 cm were similar to those of single-school summer catches in the North Atlantic Area and to single-set catches from fall school-aggregations off Long Island (cf. Figure 7).

From an analysis of length and age data for 1955 to 1958, June and Nicholson (1964) postulated that these large school-aggregations that migrated southward along the North Carolina coast in November and December comprised portions, if not all, of the stocks which had spent the summer north of Cape Hatteras, N.C. More detailed analysis of the length-age data by Nicholson (1971a) and results of tagging studies

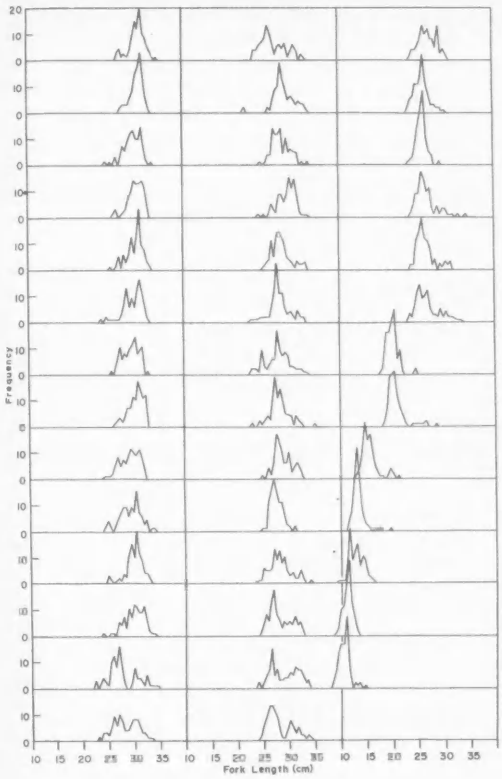

FIGURE 8.—Length-frequency distributions of Atlantic menhaden in samples from 41 single-set purse-seine catches from fall school-aggregations off North Carolina, 1955-62. The samples are arranged in order of decreasing fish length.

(Cheek et al., 1970) have confirmed and elaborated this hypothesis.

Briefly, the length-frequency data presented show a strong tendency for Atlantic menhaden to group by length. Summer schools are comprised of fish that are more nearly of the same length than is found among schools within any given area of the coast, or within the population as a whole, and there is an increase in the average length of fish within schools from south to north. Fall school-aggregations, which are usually fished only off Long Island and North Carolina, also consist of fish of similar lengths, but lengths within aggregations tend to be more variable than within summer schools.

SIZE OF SUMMER SCHOOLS IN RELATION TO FISH LENGTH

There was wide variation in the size (weight) of summer schools in relation to the average length of fish within a school. A plot of catch against mean length of fish in the 275 single-school catches (Figure 9) suggests a tendency for larger fish to occur in larger schools. The correlation between school size and mean fish length ($r = 0.144$) differs significantly from 0 ($P < 0.05$), and the relationship evidently is linear, since the arithmetic correlation coefficient is higher than that between log school size and log mean fish length ($r = 0.095$), or between log school size and mean fish length ($r = 0.103$). Comparison of the arithmetic correlation coefficients for the individual years, however, indicated heterogeneity ($\chi^2 = 17.14$; $P < 0.05$), so I plotted the data for each year separately and calculated trend lines (Figure 10). The occurrence of larger fish in larger schools is evident in some years, but in other years the trend was reversed, or there was no apparent relation between the two variables. Unequal representation of various length groups in different years may be responsible for the apparent heterogeneity of the data, but I conclude that annual

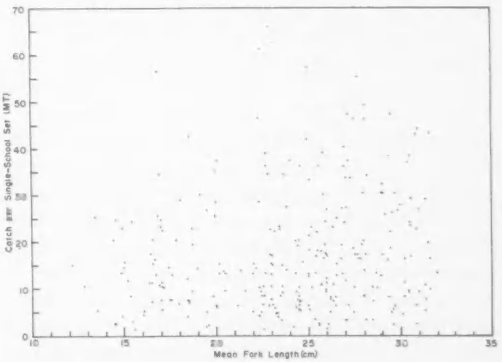

FIGURE 9.—Size of 275 single-school summer purse-seine catches of Atlantic menhaden plotted against the mean length of the fish in catch samples, 1955-62.

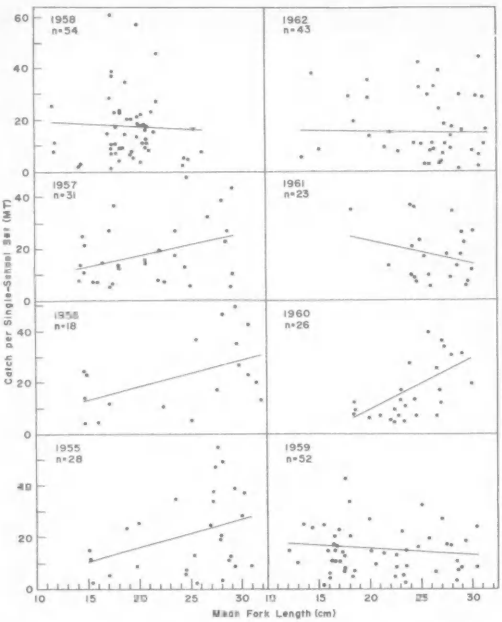

FIGURE 10.—Relationship between the size of single-school summer purse-seine catches of Atlantic menhaden and the mean length of fish in the catch sample, 1955-62.

differences in size of summer schools, which are independent of fish length, probably occur.

NUMBER OF FISH WITHIN SUMMER SCHOOLS IN RELATION TO FISH LENGTH

The number of fish within a school varied widely but, on the average, decreased as fish length increased. A plot of the estimated number of fish on the mean length of fish within the 275 single-school summer catches (Figure 11) indicates an inverse relationship between the two variables. The trend appears curvilinear; however, there is little difference among the correlation coefficients between the numbers of fish and their mean length ($r = -0.599$), between log number and mean fish length ($r = -0.597$), or between log number and log mean fish length ($r = -0.585$); all coefficients differ significantly from 0. The estimated number of fish within schools ranged from 500 (mean fish length 28.9 cm) to 655,400 (mean fish length 16.8 cm), with a mean of 86,776 fish.

In interpreting the above findings, it must be kept in mind that estimates of fish number are indirect and therefore subject to systematic bias. Furthermore, changes in the relation of school size (weight) and fish length between years were indicated in the previous section; therefore, a common regression equation may not be representative of actual changes in the numbers of fish of given size within schools. Accordingly, a trend line was not fitted to the data in Figure 11.

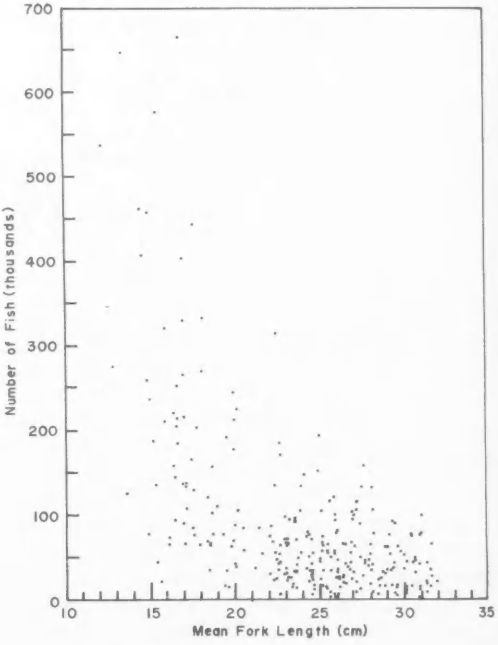

FIGURE 11.—Estimated number of Atlantic menhaden in 275 single-school summer purse-seine catches plotted against the mean length of fish in the catch sample, 1955-62.

SIZE OF SUMMER SCHOOLS IN RELATION TO APPARENT ABUNDANCE OF THE FISH

It was shown earlier that the mean single-school summer catch declined over the 8-year period in the two northern areas and fluctuated randomly in the two southern areas. To determine if these trends were an artifact of sampling or actually reflected variations in apparent abundance of the summer stock in the respective areas, I plotted the average catch per vessel week given by Nicholson (1971b) against the mean single-school summer catch in the corresponding season. There was good agreement between the two estimates in every area (Figure 12), but the relationship was closer for the South Atlantic and Middle Atlantic Areas than for the Chesapeake Bay and North Atlantic Areas. The correlation coefficient for the South Atlantic Area is significant at the 1% level and, that for the Middle Atlantic Area at the 5% level. Although the coefficients for the Chesapeake Bay and North Atlantic Areas are positive, neither differs significantly from 0. These findings indicate that summer schools became smaller as stock abundance in a given area decreased.

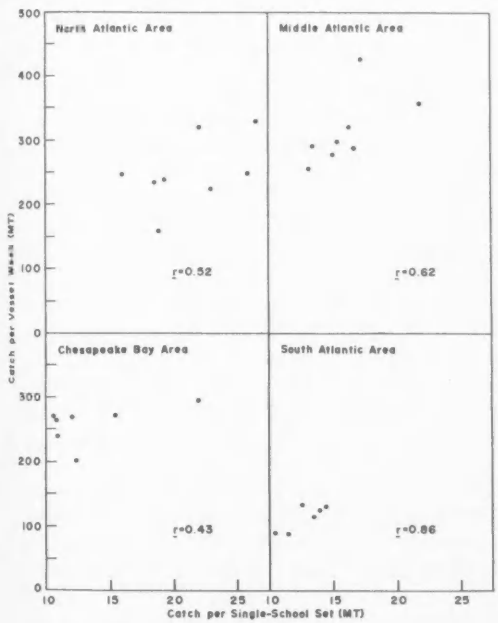

FIGURE 12.—Relationship between the purse-seine catch of Atlantic menhaden per vessel week and the mean single-school summer catch in the major statistical areas, 1955-62.

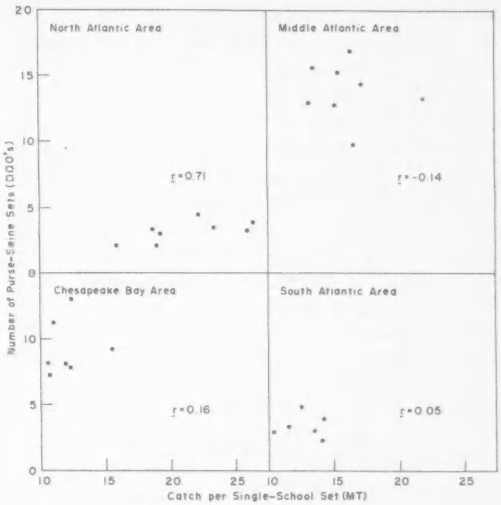

FIGURE 13.—Relationship between the estimated number of purse-seine sets for Atlantic menhaden and the mean single-school summer catch in the major statistical areas, 1955-62.

The relation between school number and school size is also of interest in assessing changes in stock abundance. A plot of the seasonal number of successful purse-seine sets (a measure of school density) given by Nicholson (1971b) on the corresponding mean single-school summer catch (Figure 13) shows a wide scattering of points within areas and considerable variability between areas. The correlation coefficient is positive for the Chesapeake Bay and North Atlantic Areas, negative for the Middle Atlantic Area, and about 0 for the South Atlantic Area, with only that for the North Atlantic Area having

borderline statistical significance ($P \sim 0.05$). If these results are real, it may be inferred from the positive correlations that larger schools were associated with greater school numbers. The negative correlation, on the other hand, suggests that schools tended to be more numerous as their average size decreased.

The reasons for the apparent discrepancies in the school density-size relationship in the different areas are not clear. The lack of any trend in the South Atlantic Area may result from variable availability of the schools. Fishermen and aircraft spotters report frequent disappearances of schools from surface coastal waters early in the day and occurrences of fish inside the extensive sounds that border the summer fishing grounds in this area (this behavior pattern of the fish may be associated with tidal currents passing through the numerous inlets and their relation to the abundant plankton food supply inside the sounds). A possible explanation for the inverse relationship between school size and number in the Middle Atlantic Area is that fishing captains tend to avoid the smaller fish and smaller schools when fish are abundant. Heavy fishing in the Middle Atlantic Area may also be a contributing factor in keeping the stock broken up into smaller schools. Fishing effort in this area averaged from 1½ to 4½ times greater than in any other area and increased by about 11% over the 8-year period (Nicholson, 1971b). There very likely is some level of fishing effort that disrupts the normal schooling habits of the fish, but the interrelationships involved appear to be much more complex than can be determined from the data in hand.

The main inference to be drawn from this section is that size of summer schools is related to stock abundance in each major fishing area. The school density-stock abundance relationship, however, needs to be clarified by analysis of data collected after 1962 when the catch dropped to the lowest levels since the 1930's.

DISCUSSION

Knowledge of the nature and consistency of groupings of Atlantic menhaden is fundamental to understanding the dynamics of the population. Results of this study demonstrated that the fishable stock occurs in schools or school-aggregations during most of the year. It is also known that the young fish school from the time of their entry into estuarine nurseries as larvae (June and Chamberlin, 1959; Reintjes and Pacheco, 1966). Thus, schooling is one of the basic behavior characteristics of this fish. June and Reintjes (1959) provided initial evidence that the fish school by size and to some extent by age and also showed that schools in a given locality more closely resemble each other in composition than schools from different localities. June and Nicholson (1964) and Nicholson (1971a) described in some detail the increase in average length and age of the fish with increased latitude and inferred annual north-south movements of the fish from seasonal changes in their length and age distributions. The findings of this paper support the conclusions of the foregoing studies and provide further insight into the variability of the distribution, composition, and size of summer schools and fall school-aggregations. But one of the critical unknowns is the extent to which such variability is related to stock density and, ultimately, to fishing.

Evidence presented here indicates that the size of summer schools is a function of stock abundance. It was also shown that an inverse relationship existed between fish length and size (weight) of summer schools. These findings suggest that there probably is an optimum school size for fish of given length that is most favorable for survival. If so, there must be a level below which the population must not be fished without running the risk of disrupting schooling to the point of inflicting irreparable damage to population resilience. While these hypotheses are unprovable with present data, the inference is that schooling marine fishes that are sought by surface sightings are more vulnerable from unregulated fishing than nonschooling species that are not subject to direct observation. Slight changes in the nature and consistency of grouping of Atlantic menhaden ought therefore to be considered in assessing both short- and long-term effects of fishing on the population.

The inverse relationship shown between fish length and the number of individuals within

summer schools also has important implications in regard to the yield that may be expected at different levels of fishing and to the well-being of the population. Since the fish are differentially distributed by length, with smaller fish occurring in the South Atlantic and Chesapeake Bay Areas during the greater part of the year, a disproportionate increase in the fraction of the population taken in these areas would be expected to result in a substantial reduction in the stock of larger fish available in the Middle and North Atlantic Areas. Putting it another way, a given unit of effort in the two southern areas imposes a higher fishing mortality rate. Moreover, immoderate fishing on the recruit stock in the two southern areas may also be expected to result in a drastic reduction in the size of the spawning stock. Thus, a stock-recruitment model that incorporates information on school size, number, and composition is less likely to fall short of realistic estimates of the levels of fishing commensurate with a desirable population structure and the optimum catches that may be expected therefrom.

If the role of schooling in the dynamics of the Atlantic menhaden population is to be understood, the research must be based on broader considerations than the classical methods of stock assessment. Limiting interpretation of changes in the population to simple relationships between fishing effort and catch is to ignore the dynamic aspects of fish schooling implied throughout this paper. Because of the selective nature of purse-seine fishing, fishermen's logbooks and catch records can only furnish indirect evidence of changes in the behavior and habits of the fish due to fishing. Furthermore, increased efficiency in the methods of menhaden fishing, coupled with technical improvements in fishing gear and vessels, has greatly altered long-term measures of effective fishing effort with the probable result that fishing mortality tends to be underestimated and changes in schooling of the fish minimized or perhaps obscured. Thus, there is a primary need for direct measures, independent of fishing, of school biomass and number and distribution of schools in the sea, including correlative measures of the fall school-aggregations off Long Island and North Carolina. With menhaden, direct aerial observations or photography and remote sensing are practicable (see, e.g., Roithmayr, 1970). Recent advances in underwater acoustical techniques (see, e.g., McClendon, 1968; Smith, 1970; Love, 1971) offer a supplementary means of identifying and quantitatively assessing the size and composition of menhaden schools.

Finally, development of a fully analytical approach to the role of schooling in the study of the dynamics of the Atlantic menhaden population requires a broad spectrum of information on the behavior of the fish in relation to environmental factors and other fishes. Briefly, what is needed is a more or less continuous picture of what the schools are doing. Included here are (1) the nature of short-term, i.e., day to day, changes in the behavior, structure, and distribution of summer schools in response to changes in light, salinity, temperature, currents, and food conditions, (2) the behavior of schools in isolation and in association with other fishes, (3) the primary mechanisms involved in the formation of school-aggregations and the seasonal migrations, and (4) the winter habits and whereabouts of the fish. There, for example, are no published data from which it is possible to estimate the swimming speed or endurance of which a school is capable in escaping a predator or a net. Much information can be provided from direct observations on the fish in free-swimming schools under a variety of life conditions. Aircraft are routinely employed in locating and directing fishing operations (Squire, 1961; June, 1963), yet little use has been made in menhaden research of either the information compiled by individual fish spotters or the facilities offered by the aircraft fleet. In practice this might simply require the recording of aerial observations during fishing operations and special reconnaissance flights as a means of assessing changes in the distribution and size of schools or school-aggregations during the fishing season, or mapping the migrations of this fish. Ancillary data on the behavior and physiology of the fish may be generated from experimental studies in aquaria, artificial ponds, and temporary enclosures in the sea. Any single approach to the study of schooling of Atlantic menhaden has

limitations, but a combination of methods, such as those outlined here, can lead to better understanding of the obligatory nature of schooling and its role in vital life processes of individuals and dynamics of the population.

EPILOGUE

This study was planned and most of the tabulations of data and writing completed before I left the Menhaden Program in 1964, but because of the press of other duties, I was unable to fulfill an obligation to finish the work earlier. My resolve to complete it at this time was renewed when I received Dr. Reuben Lasker's letter to former associates of Dr. Elton Sette soliciting papers to be included in this dedicatory issue of the *Fishery Bulletin*.

Some of the ideas contained in this study were inspired by Dr. Sette's papers dealing with the Atlantic mackerel and the Pacific sardine and from my discussions with him of apparent similarities in the behavior and biology of the Atlantic menhaden and the Pacific sardine. It indeed is a privilege for me to acknowledge, in this place, my appreciation of Elton's influence on my concept of the disicplines of fishery biology, his sharing of an interest and enthusiasm for tropical botany and color photography, and lastly his challenging opposition on the tennis court.

ACKNOWLEDGMENT

I wish to thank Mary K. Hancock, who compiled the menhaden vessel logbook records and assisted in processing the basic catch-sample data used in this study.

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ACTIVITY OF HAWAIIAN REEF FISHES DURING THE EVENING AND MORNING TRANSITIONS BETWEEN DAYLIGHT AND DARKNESS

EDMUND S. HOBSON[1]

ABSTRACT

Activity during the morning and evening transitions between day and night was studied as part of a broad investigation of ecological relations among reef fishes in Kona, Hawaii, during 1969 and 1970.

Most of the fishes are either diurnal or nocturnal, the former being mainly inactive at night, the latter mainly inactive in daylight. During active periods their behavior is dominated by feeding, whereas inactive periods are dominated by measures to enhance security. Thus twilight behavior involves primarily a changeover from feeding to sheltering, and the reverse. Migrations of various types between shelter locations, where they rest, and feeding grounds are a major element of the transition periods.

The transition events proceed in an established, well-defined sequence. In the evening, after the diurnal fishes have descended to shelter and before the nocturnal fishes have risen into the water column, there is an interim period of about 20 min during which both diurnal and nocturnal fishes are close to the substrate; it is at this time that reef fishes are most vulnerable to predators, and the proximity of cover offers protection. Similar behavior occurs among related fishes in the Gulf of California. The interim period in Kona corresponds in time relative to sunrise and sunset to the period during which schooling fishes in the Gulf of California are under heaviest attack; however, because schooling fishes and the predators that exploit them are not major elements of the Kona fauna, overt predator-prey interactions are not prominent there. Thus the well-ordered pattern of events that characterizes twilight in Kona also occurs on other reefs widespread in tropical seas, whether or not there exists in each of these areas today a severe threat from large piscivorous predators. The twilight pattern of actions is the result of a long evolution that in any one area transcends the existing situation and species. Because predator-prey interactions among fishes have been influenced throughout time by certain basic and unchanging phenomena, the similarity of twilight activity patterns among fishes on widely separated reefs today reflects the impact of a historic threat from predators.

Most fishes on tropical reefs are active either by day or by night, with the diurnal species mostly inactive in darkness and the nocturnal species mostly inactive in daylight (Hobson, 1965, 1968; Starck and Davis, 1966). The changeover from one situation to the other is a complex process, with events following a well-defined sequence. This report describes the significant events during the evening and morning transition periods in Kona, Hawaii, between June 1969 and August 1970. It is a segment of a broad study of ecological relations among Hawaiian reef fishes. The present report, which deals with the twilight situation, will be followed by a second report covering the situations throughout day and night, respectively, and including a detailed analysis of food habits (Hobson, in preparation). Some highlights of this program were outlined earlier (Hobson, 1970).

METHODS

This study is based on observations that spanned evening twilight on 20 occasions and

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morning twilight on 18 occasions. Generally over 2 hr were spent on station during each observation period, although the transition events detailed in this report were concentrated into a span of about 1 hr, as discussed below. Before the data presented in this report were collected, general observations in the study area at these times of day had provided a broad understanding of the twilight transition. Also contributing significantly to this understanding were extensive observations made during twilight in other seas, especially in the Gulf of California (Hobson, 1965, 1968), where related fishes have similar behavior. With this background and using scuba, I was able to recognize and record what I knew to be significant events and to note the time and other associated characteristics. Additionally, some data from observations made at various times of day and night during other segments of the program in Kona are pertinent to the present report and thus used here. Furthermore, interpretation of the twilight activities benefited significantly from these other phases of the overall Kona program.

Throughout all twilight observation periods, Lloyd D. Richards, stationed on the sea floor nearby, recorded incident light in foot-candles each minute with a photometer facing the water's surface. In this report, all records of light levels during specific events refer to these readings. To minimize instrument error, two photometers of the same model (Weston Ranger 9, universal exposure meter, Model 348)[2] were alternated. The accuracy of the absolute values obtained with these inexpensive instruments is not considered critical; rather, the primary concern is that the relative values are consistent, thus permitting comparisons of behavior relative to time and light between one observation period and another.

The time of specific events are presented relative to time of sunrise or sunset, as calculated for the longitude and latitude of the study area using the Nautical Almanac, U.S. Naval Observatory. An event occurring at about the same time each day relative to sunrise or sunset, will, in time of day, vary by as much as several hours over the course of the year. This fact reduced any bias that might have resulted from subconsciously looking for an event at a specific time. Although I was alert for certain events in sequence, based on familiarity with the general situation, I consciously avoided thinking in terms of time relative to sunrise or sunset during the observations. This was not difficult to do. I did not calculate time of sunrise or sunset until after a period of observation, and neither could have been directly observed, even had I not been underwater at the time; in the study area a large volcano blocks much of the eastern sky, and the western sky generally is obscured by clouds at the end of the day. Furthermore, usually a week or more elapsed between observations of morning or evening twilight, so that the time of sunrise and sunset changed substantially from one set of observations to the next. Finally, I did not translate the data from time of day to time relative to sunrise or sunset until the program in Hawaii was completed.

Obviously all events judged significant were not witnessed during each observation period. Many were evident only in certain locations, and several occurred at about the same time. Consequently, the number of times that data were recorded for each event varies widely.

Names used for the fishes generally follow those given by Gosline and Brock (1960); exceptions occur where more recent taxonomic studies have indicated changes. Most of the fishes are referred to some broad feeding category, such as being a herbivore, a plankton feeder, etc. These general designations are based on detailed study of food habits to be reported elsewhere (Hobson, in preparation).

In parentheses following the first mention of each fish species are given a mean and range of standard lengths, for example (235: 173-284 mm). These figures represent the sizes of specimens of that species that were collected for the food habit analysis (Hobson, in preparation). In collecting these specimens an attempt was made to sample individuals of sizes that showed behavior of adults. Hence these figures provide a good measure of the relative sizes of

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

the different species, as relating to the activity described in the present report. This information is important because the size of a given fish is reflected in its behavior during twilight, as discussed below.

A number of species prominent on Hawaiian reefs are not mentioned in this report. My coverage is confined to species in which I recognized behavior relating specifically to the twilight transition period on the three reefs where twilight behavior was studied. Some other species not prominent on these reefs are abundant elsewhere and were studied during other phases of the overall project. These other segments of the work in Kona yielded no data inconsistent with what is reported or discussed below.

STUDY LOCATIONS

The reef habitat on the Kona coast is restricted to a narrow shelf close to shore. From the base of a rough, basalt shore cliff, the sea floor in most locations slopes gently downward for distances of between 50 and 600 m from shore. At this point, where the water is generally about 20 to 25 m deep, the bottom drops abruptly to great depths.

Most of the data for this report were collected from three inshore locations, all at depths between 5 and 10 m. Each location has a distinctly different substrate. Station 1 is in Kealakekua Bay among massive heads of the coral *Porites pukoensis* rising 2 to 3 m above the sea floor. Station 2 is in Honaunau Bay among an extensive field of the coral *Porites compressus* growing in fingerlike branches 10 to 15 mm wide. Station 3 is also in Honaunau Bay, but among massive basalt boulders 2 to 3 m across that are largely overgrown with encrusting algae and corals. These boulders are variably interspersed with the forms of both *P. pukoensis* and *P. compressus* described above.

The remarkably constant weather and water conditions that characterize the Kona coast held true throughout the 15 months of observations. Consequently, variables inherent in changing environmental conditions were minimized, making it easier to recognize activity patterns associated with the twilight transition periods.

TRANSITION FROM DAY TO NIGHT

It is difficult to determine exactly when the daytime situation begins to move toward that prevailing after dark. In large part, this difficulty reflects variations in activity of many diurnal fishes because of differing water transparencies, and even more when variable cloud cover causes light levels to fluctuate. These variations are difficult to distinguish from those associated with the lesser light levels of the advancing afternoon. Additionally, as the day progresses, activity of diurnal fishes changes subtly in many other ways that may or may not relate to a transition to the nocturnal mode. The situation prevailing throughout the day (Figure 1), including variations with changing light levels and other factors, is described elsewhere (Hobson, in preparation). This report is concerned with the more striking transformations that occur during the transition between daylight and darkness, beginning about 15 min before sunset and lasting until about 45 min after sunset—a span of about 1 hr. Three major periods are readily recognized: 1) the cover-seeking of the diurnal fishes; 2) an interim period; and 3) the mass emergence of nocturnal species.

COVER-SEEKING OF THE DIURNAL FISHES

Initial Overt Phase of the Transition

An early cue to the developing transition lies with the plankton-feeding fishes that swim during the day in stationary aggregations up in the water column. Prominent among these are the damselfishes *Abudefduf abdominalis* (142: 105-162 mm), *Chromis leucurus* (57: 37-70 mm), *C. ovalis* (124: 121-138 mm), *C. vanderbilti* (38: 17-46 mm), and *Dascyllus albisella* (79: 42-95 mm). The distance of each fish from the substrate is related to its size, because the larger individuals swim at higher levels in the water column. These fishes descend progressively closer to the sea floor as light diminishes. Members of the smallest species, *Chromis vanderbilti*, are the first to take cover; they seldom move more than a meter above the reef on even the

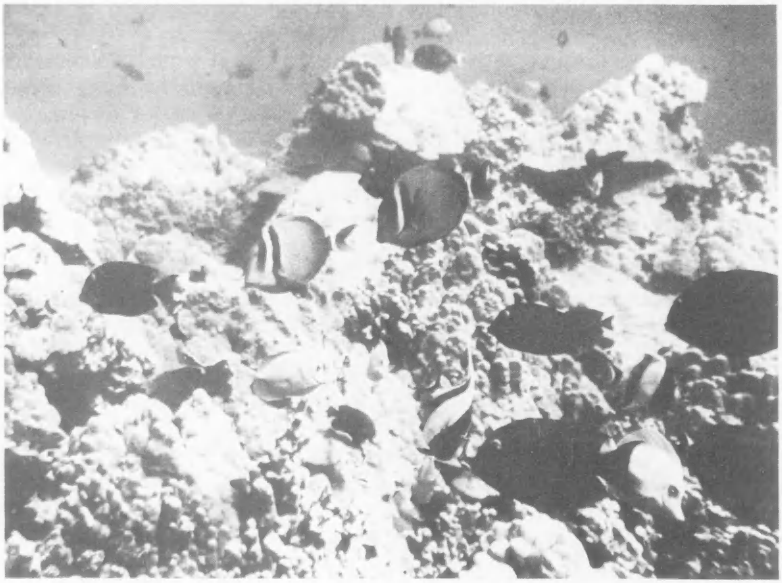

FIGURE 1.—Daytime on a coral reef in Kona, Hawaii. Most of the fishes are acanthurids, including *Ctenochaetus strigosus*, *Acanthurus leucopareius*, and *Zebrasoma flavescens*. Other fishes include *Centropyge potteri* and *Zanclus canescens*.

brightest days, and by 15 min before sunset all of them have dispersed among holes in the reef. The progressive descent of the other plankton-feeding damselfishes is treated below.

As individuals of *C. vanderbilti* are taking shelter, the transition to the nocturnal situation is clearly underway. The numbers of smaller wrasses active on the reef have been noticeably declining since at least 30 min before sunset, though many still remain in view. More obvious, an increased tendency to aggregate is exhibited by some of the smaller herbivorous fishes, including the surgeonfishes *Acanthurus nigrofuscus* (120: 100-140 mm) and *Ctenochaetus strigosus* (125: 110-145 mm) and also the parrotfish *Scarus taeniurus* (210: 180-243 mm). These aggregations continue to develop through sunset and into early twilight.

By about 5 min after sunset the last individuals of many diurnal species have taken cover, including the last of the smaller wrasses. No data are available on precisely when the larger wrasses seek cover (those exceeding a length of about 350 mm are uncommon in the study areas). Nevertheless, my observations agree with those of Gosline and Brock (1960), who stated that all Hawaiian labrids are inactive at night.

Two species of smaller labrids are representative: *Thalassoma duperrey* (125: 103-146 mm) and *Labroides phthirophagus* (63: 33-91 mm). (I did not collect specimens of the latter species —size data are from Youngbluth, 1968.) *T. duperrey* probably is the most numerous of the readily observed species of fish overall in the various Hawaiian reef habitats and thus serves well as an indicator species. *L. phthirophagus* is not abundant, but as a cleaner fish that centers its activity around well-defined stations (Randall, 1958; Youngbluth, 1968), individuals can be readily recognized from one evening to another.

Observations on Thalassoma duperrey.—On five occasions I was confident that I observed

the last individual of *T. duperrey* active in my immediate area take shelter (Figure 2). Each of these individuals swam in and out of coral crevices several times before finally slipping into a hole where it remained. On subsequent close inspection I found each one lying on its side in the hole, and intermittent checks over the next hour disclosed each still in the same position. Following one such observation, a predawn inspection the next morning found the fish in the same spot.

There is evidence that, on a given evening, an individual is intent on resting in a particular spot. Two incidental observations give credence to this view. One evening I lay prone and immobile across a large coral head (*Porites*), watching the many *T. duperrey* around me, and waiting to note the last one that took cover. The behavior of one individual was unusual: it circled close by regarding me more intensely than seemed normal, then swam away. Several times this same fish reappeared, repeated this behavior, then swam away again. Curious, I abandoned my position and followed when the fish reappeared. After being led in a circle, I found myself back at the original location, where the fish slipped into a coral crevice in the spot where I had been lying. Only then did it occur to me that this fish had behaved abnormally probably because I had been blocking entry to its nocturnal resting spot. Other individuals of *T. duperrey* were still active in the area when this incident occurred, making it uncertain whether the fish actually had been delayed in attaining cover. A similar incident later was more conclusive. Again, I rested motionless, watching the many individuals of this labrid during the evening transition period, this time leaning against a vertical wall of coral (*Porites*). One individual swam close by, then moved to a low ledge about 2 m away, where it then swam back and forth, watching me continuously. Several times it momentarily left the ledge, approached me, and then darted back to the ledge. Recalling the earlier incident, I did not move from my station until long after all other fish of this species had gone under cover. Finally, 12 min after sunset (light 0.8 ft-c), with the behavior of the labrid under observation still unchanged, I moved away. Immediately, it swam to my former location and slipped into a crevice. Later, using a light, I could see this wrasse lying on its side, wedged back in the crevice. (These two incidents are not included among the data represented in Figure 2, which includes only situations judged normal.)

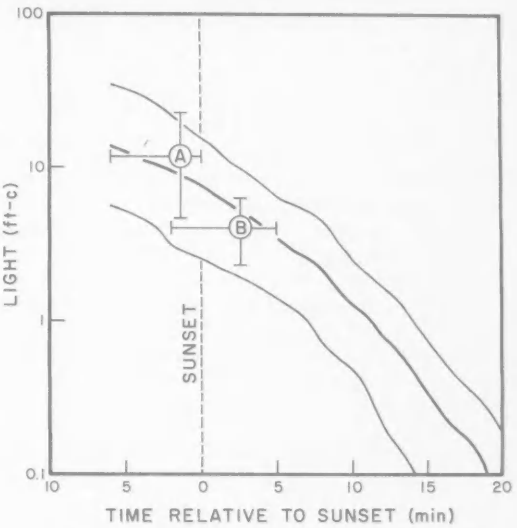

FIGURE 2.—Some characteristics of certain labrids during evening twilight. Each lettered symbol represents a species: A. *Thalassoma duperrey*—when the last individual took cover on five evenings. B. *Labroides phthirophagus*—when one individual took cover on five evenings. The circle represents mean values of both time and incident light when the event occurred; the vertical line, the range of incident light values; and the horizontal line, the range in time relative to sunset. The three diagonal lines represent: the maximum light values for each minute relative to sunset during all evening twilight observation periods (top line), the minimum values for each minute (bottom line), and the mean values (heavy median line).

These observations indicate that a fish can have a strong affinity for a specific resting spot. However, I have no evidence that this is more than a short-term phenomenon. Many nocturnal resting spots of *T. duperrey*, and other fishes, were discovered incidentally during other phases of the work in Kona when I closely inspected crevices in the coral during the night. When circumstances permitted, followup observations

were made at various times during subsequent nights. Although a given resting spot was frequently occupied over several nights by what seemed to be the same fish, this did not hold true for longer than a week or so. I doubt that my repeated intrusions disturbed these fishes sufficiently to influence a change of location. Usually a spot occupied by a resting fish on one evening was vacant when next observed on a subsequent night.

Observations on Labroides phthirophagus.—Individuals of this species, like other labrids, seek cover for the evening during the period from immediately before to just after sunset. *L. phthirophagus*, like *T. duperrey*, finds nocturnal shelter in crevices of rock or coral. But with this species, unlike the others, individuals can readily be recognized from one day to the next, owing to their close association with well-defined cleaning stations. Thus, whereas observations of *T. duperrey* each evening involved only the last active member of the species, the cover-seeking of one particular individual *L. phthirophagus* was timed over five different evenings (Figure 2). The one instance when this fish took shelter 5 min after sunset was the latest that any of the smaller labrids were seen active.

L. phthirophagus cleans other fishes at its station until it takes shelter. Frequently other species still hover at the station in soliciting fashion (see Losey, 1971) after the resident cleaner has retired for the night.

Twilight Upsurge in Activity

Visible activity among many diurnal fishes rises sharply at about the time of sunset. However, feeding generally is not involved; rather, the upsurge stems mostly from the many species on the reef that migrate from one location to another at this time, and also to increased interspecific and intraspecific aggression, at least much of which is related to territoriality. In addition, some species show at this time an increased tendency to aggregate and to swim in more visible locations.

Above, I note that prior to sunset some of the smaller herbivores increasingly aggregate a meter or so above the reef. Beginning with this event, the phenomenon gains momentum, encompassing more and larger fishes, especially among the surgeonfishes and parrotfishes. By 5 min after sunset this activity has reached its maximum level, even though most of the smaller species among which it first appeared by then have discontinued the activity and have settled under cover.

There seem to be two major types of aggregations: Assemblages of one type, often of mixed species, mill about 1 or 2 m above certain parts of the reef; and assemblages of the other type, mostly of a single species, move with seeming purpose from one location on the reef to another. Each of these types of assemblages is treated separately below.

The milling assemblages.—During about a 10-min period, 5 to 15 min after sunset, the scene on many parts of the reef is dominated by large, essentially stationary, mixed-species aggregations that mill about in certain locations 1 or 2 m above the substrate. Various surgeonfishes predominate, especially *Zebrasoma flavescens* (163: 130-195 mm), *Acanthurus achilles* (182: 165-200 mm), *A. nigroris* (165: 130-180 mm), *A. leucopareius* (190: 185-210 mm), and *Naso lituratus* (180: 156-220 mm). Also prominent are the parrotfish *Scarus sordidus* (230: 205-260 mm), the triggerfishes *Melichthys niger* (165: 122-195 mm), and the filefish *Cantherines dumerili* (200: 171-240 mm).

The twilight migrations.—Some members of many species migrate at this time from one location on the reef to another. Although the patterns remain obscure, this activity involves movements that occur consistently in certain locations. Evening after evening specific routes are followed, in which certain species stream continuously past a given point in long drawn-out processions over a period of several minutes.

Prominent participants include members of certain species, including the surgeonfish *Naso hexacanthus* (261: 202-392 mm) and the damselfish *Chromis verater* (120: 100-141 mm), that feed on plankton during the day high in the

water column at the outer edge of the reef. Many of these fishes show a migratory pattern up into the shallower parts of the reef at nightfall, but the pattern is obscured by the circumstance that other individuals of these same species do not move inshore, but instead remain throughout the night at the outer edge of the reef, nestled among the coral on the sea floor below their midwater feeding areas.

Many of the smaller herbivores, including the surgeonfishes *Zebrasoma flavescens* and *Ctenochaetus strigosus*, as well as the parrotfish *Scarus sordidus*, exhibit similar movements. These patterns are obscured because on any given night relatively few individuals of these species join such migrations; many others of the same species do not, including some that are prominent in the milling assemblages noted above. It remains unknown just what sort of redistribution pattern is achieved by these movements.

Descent of the Plankton-Feeding Damselfishes

Individuals of the smallest plankton-feeding damselfish *Chromis vanderbilti* have scattered among the rocks by about 15 min before sunset, as noted above. During the few minutes immediately following sunset, members of the next smallest species, *C. leucurus*, settle individually in coral crevices. On three evenings the time and light levels were recorded as the last individual of *C. leucurus* in my surroundings took shelter (Figure 3).

The larger species, including *Abudefduf abdominalis*, *Chromis ovalis*, *C. verater*, and *Dascyllus albisella*, continue to drop lower in the water column throughout this period. Precise times for the different stages of the descent are not available, but all drop at a similar rate, a fact probably related to their similar sizes. The descent begins well before sunset, when individuals in 8 m of water, for example, are about 5 m over the sea floor. At 8 to 10 min after sunset they are about 1 to 2 m over the coral, and here contribute to the general activity, where the milling aggregations and migrating schools, described above, dominate the scene.

Vacating the Water Column

Throughout the time that the milling aggregations and migrating schools swim over the reef, individuals from these assemblages are descending to cover below. Nevertheless, a substantial number still swim in the water above the reef, along with the small groups of larger plankton-feeding damselfishes, at about 10 to 15 min after sunset. Then, abruptly, the vast majority of these fishes suddenly drop to the reef below, leaving the water column essentially deserted. This is a well-defined phenomenon, and on 12 evenings the time and light were recorded when it occurred (Figure 3).

Cover-Seeking of Other Diurnal Fishes

Also going under cover at about the time that the water column is vacated are the larger parrotfishes *Scarus rubroviolaceus* (366: 267-475 mm) and *S. perspicillatus* (348: 269-463 mm).

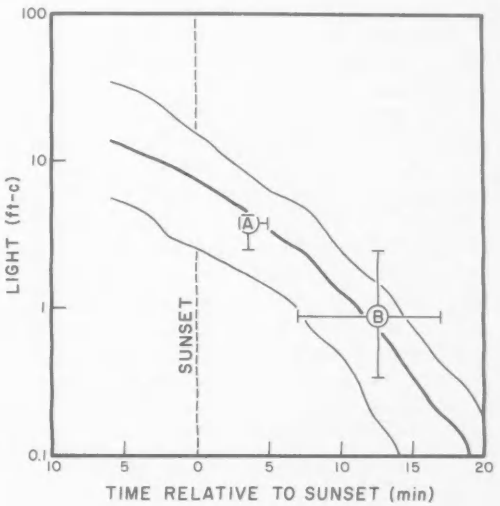

FIGURE 3.—Some characteristics of certain diurnal fishes during evening twilight. A. *Chromis leucurus*: when the last individual took cover on three evenings. B. When the water column was abruptly vacated by diurnal fishes on 12 evenings. For explanation of symbols, see legend for Figure 2.

The smaller parrotfishes had sought shelter earlier. Gone now too are the triggerfishes *Sufflamen bursa* (140: 109-164 mm) and *Rhinecanthus rectangulus* (142: 114-170 mm), as well as the filefishes *Pervagor spilosoma* (85: 64-120 mm) and *Cantherines sandwichiensis* (116: 84-132 mm), all of which had remained close to the substrate throughout their active periods during daylight and early twilight. Because most of these and many other diurnal species are not especially numerous on all of the study areas, often none are in view for long periods even during those times of day when they are most active; therefore, it would not have been meaningful to record the last individual of each species that was seen to take cover, as was done with the ubiquitous *Thalassoma duperrey* and a few other species treated in this report. This procedure is meaningful only with species whose members are so numerous and widespread that in all study areas some of them are always in view during their active periods. Nevertheless, these species, as described above, are only rarely seen in exposed positions after the water column has been vacated.

Many sedentary diurnal fishes find shelter during this period too. One suddenly realizes that such species as the hawkfishes *Paracirrhites forsteri* (139: 93-181 mm), *P. arcatus* (82: 49-101 mm), and *Cirrhitops fasciatus* (76: 39-91 mm) are only occasionally visible in locations where they are numerous during daylight. The same is true of the blennies *Exallias brevis* (94: 70-106 mm) and *Cirripectus variolosus* (73: 66-80 mm). Relative activity in species that are at least overtly inactive is difficult to quantify. Nevertheless, after the nocturnal situation prevails, about 30 min after the free-swimming fishes vacate the water column, these sedentary diurnal fishes rarely occur in exposed positions.

THE EVENING INTERIM PERIOD

When the last of those diurnal fishes swimming above the coral abruptly descend to the ocean floor, about 10 to 15 min after sunset, the evening interim period begins. At the outset, many diurnal fishes still mill about in pockets among the coral, close to the substrate. Prominent among these are the medium-sized surgeonfishes, such as *Acanthurus achilles*, that were prominent in the milling aggregations earlier. In addition, a few of the larger surgeonfishes, like *A. dussumieri* (340: 302-390 mm), still swim slowly over the coral in small scattered schools, but these do not diminish the prevailing quiescence. The closely related moorish idol, *Zanclus canescens* (108: 74-137 mm), still swims in groups of three or four, but close to the substrate. The butterfishes, family Chaetodontidae, often remain paired, as during midday, but some already show colorations that are different from those seen in daylight; these include *Chaetodon auriga* (151: 132-160 mm), *C. ornatissimus* (119: 95-140 mm), *C. multicinctus* (84: 78-94 mm), and *C. unimaculatus* (85: 66-102 mm), which become progressively less active and stay close to the coral. Damselfishes too, including *Pomacentrus jenkinsi* (89: 80-100 mm), and *Plectroglyphidodon johnstonianus* (60: 39-70 mm), though generally solitary, remain active close to coral and rock shelter at this time. The chaetodontid *Centropyge potteri* (80: 69-86 mm) behaves much like these damselfishes.

Into this situation of rapidly diminishing activity among diurnal species, the nocturnal species begin to emerge from the caves and crevices of the reef, in which they have passed the daytime. The first to appear is the cardinalfish *Apogon snyderi* (96: 82-130 mm), which remains close to the substrate, frequently mixing with the diurnal species that are settling there. A second cardinalfish, *A. menesemus* (114: 90-134 mm), soon follows its congener into the open. The initial sightings of *A. snyderi* and *A. menesemus* moving away from shelter were recorded on four and five evenings, respectively (Figure 4).

Several minutes later, when the diurnal species still in view are becoming more and more quiescent, the first of the squirrelfishes, the relatively large *Holocentrus sammara* (162: 128-202 mm), appears. This event was recorded on four evenings (Figure 5). Throughout the day, some individuals of both *A. snyderi* and *H. sammara* hover in view at the entrances to their diurnal retreats; consequently, one must be thoroughly familiar with these fishes to recognize

the subtle behavioral distinctions that characterize their initial moves away from shelter in the evening.

The interim is aptly termed the "quiet period," because so little activity is visible to an observer. The small fishes, both diurnal and nocturnal, are close to the sheltering substrate at this time. The term "quiet," as used here, refers to an absence of observable activity, not to an absence of sound. In fact, vocalizing of many animals increases throughout the transition period (see, for example, Cummings, Brahy, and Herrnkind, 1964).

During the latter part of the interim, or quiet, period, a few individuals of *Myripristis* spp. move out of their caves but stay close to the substrate. When the members of these species suddenly boil out of their caves 30 to 35 min after sunset, this striking event marks an abrupt end to the evening interim period.

THE MASS EMERGENCE OF NOCTURNAL FISHES

Reoccupation of the Water Column

The darkening water column suddenly becomes reoccupied by a horde of fishes when squirrelfishes of the genus *Myripristis* come streaming out of their diurnal retreats. The timing of this spectacular event was recorded on eight different evenings (Figure 5). Three species prominent on the study reefs, *Myripristis argyromus* (176: 116-210 mm), *M. multiradiatus*

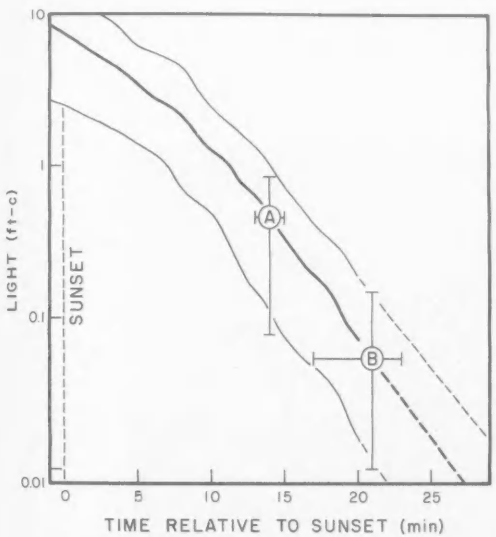

FIGURE 4.—Some characteristics of certain apogonids during evening twilight. A. *Apogon snyderi*: when the first individual left cover on four evenings. B. *Apogon menesemus*: when the first individual left cover on five evenings. For explanation of symbols, see legend for Figure 2. In addition, the broken diagonal lines represent estimated light values. Because of instrument limitations, light readings later than about 20 min after sunset were often unreliable, and therefore values beyond this point were estimated by projecting the established lines.

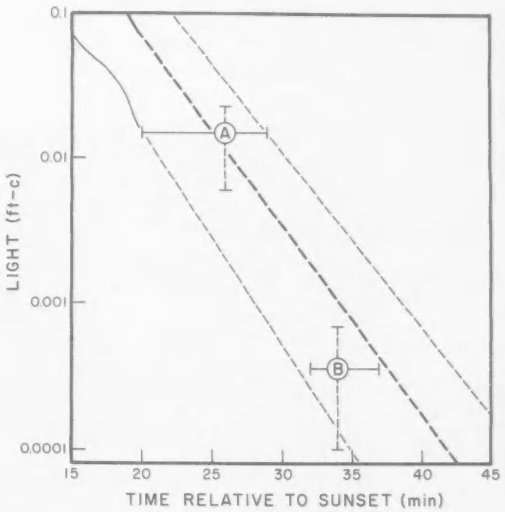

FIGURE 5.—Some characteristics of certain holocentrids during evening twilight. A. *Holocentrus sammara*: when the first individual left cover on four evenings. B. *Myripristis* spp: when large numbers of these fishes abruptly appeared in the water column on eight evenings. For explanation of symbols, see legends for Figures 2 and 4. In addition, broken lines representing range of light values in species symbols indicate that these were estimated for each observation by projecting the established line beyond 20 min after sunset.

(120: 74-145 mm), and *M. berndti* (169: 136-270 mm), all emerge at the same time. All move right up into the water column, although *M. multiradiatus*, the smallest of the three, stays closer to the reef than the other two. Almost immediately, many individuals of *M. argyromus* and *M. berndti* move offshore in mass. That fishes of this genus migrate offshore at night was noted by Gosline (1965), and their nocturnal plankton-feeding habits have been established (Hobson, in preparation).

At about the same time, bigeyes, *Priacanthus cruentatus* (173: 115-255 mm), rise from the rock and coral crevices that had sheltered them in daylight and, forming schools high above the reef, most of them swim offshore. The offshore migration at night by *P. cruentatus* was noted by Gosline (1965), and the feeding habits of this fish were studied (Hobson, in preparation).

At about the same time that fishes are reoccupying the water column, many other nocturnal fishes that are active only close to the substrate begin to be seen for the first time. These are mostly small species under about 200 mm long, and all are predators. Included are a number of squirrelfishes of the genus *Holocentrus*, including *H. xantherythrus* (106: 88-123 mm), *H. diadema* (109: 85-127 mm), *H. lacteoguttatus* (88: 52-104 mm), *H. tiere* (141: 67-235 mm), and *Holotrachys lima* (91: 70-113 mm); also the scorpionfishes *Dendrochirus brachypterus* (99: 80-118 mm), *Pterois sphex* (83: 58-121 mm), and *Scorpaena coniorta* (46: 26-67 mm), and the brotulid *Brotula multibarbata* (169: 73-250 mm). The nocturnal feeding habits of these fishes were studied (Hobson, in preparation).

To the human eye, it is nighttime on the reef at about 50 min after sunset, although the last vestige of daylight is still visible on the water's surface overhead. By this time the nocturnal situation prevails and will continue to do so until morning (Figure 6).

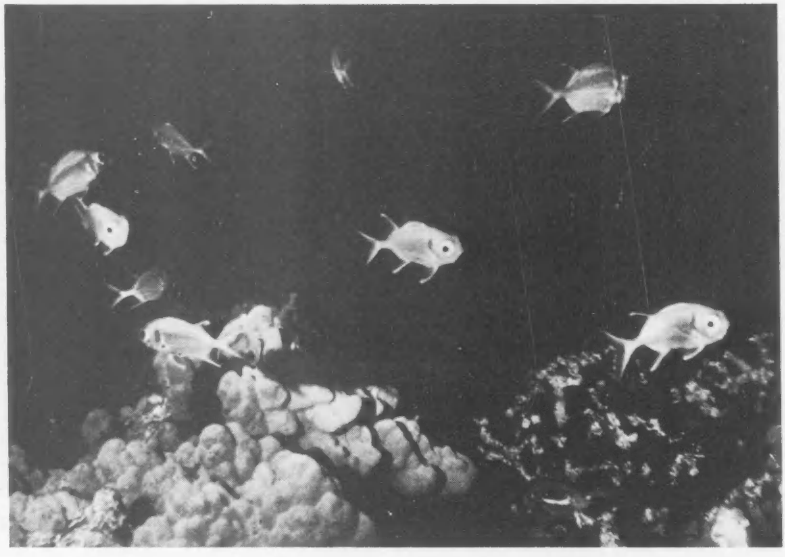

FIGURE 6.—Nightime on a coral reef in Kona, Hawaii. The fishes swimming above the reef are squirrelfish, *Myripristis* spp. At lower right center a single surgeonfish, *Zebrasoma flavenscens*, is nestled among the coral; the horizontal white bar on its side is, in adults, a feature of its nocturnal coloration.

TRANSITION FROM NIGHT TO DAY

As is true of the transition from day to night, it is difficult to determine exactly when the nighttime situation begins to give away to that prevailing during daylight. In large part, this difficulty reflects the great variation in activity among fishes at night relative to the amount of moonlight. The situation throughout the night, including variations under different levels of moonlight, is described elsewhere (Hobson, in preparation). This report is concerned with the more striking transformations that occur during the transition from darkness to daylight, beginning about 45 min before sunrise and lasting until about 15 min after sunrise—a total of about 1 hr. As is true of the evening transition, described above, three major periods are readily recognized: 1) the cover-seeking of the nocturnal fishes; 2) the morning interim period; and 3) the mass emergence of diurnal species.

COVER-SEEKING OF THE NOCTURNAL FISHES

Return of the Offshore Feeders

When there is no moonlight, an underwater observer notices the first trace of sunlight on the waters surface overhead about 1 hr before sunrise. Nevertheless, not for another 10 to 15 min do the fishes display overt signs that the transition to their daytime behavior is underway. Then, about 40 to 50 min before sunrise, the numbers of *Myripristis* spp. and *Priacanthus cruentatus* increase sharply near the caves where they pass the daylight hours. To some extent this is the assembling here of those individuals that had remained on the reef during the night, but mostly this marks the return to the reef of individuals that had migrated elsewhere.

The species of *Myripristis* become simultaneously so abundant everywhere that it is uncertain to what extent they have arrived together in schools or have converged simultaneously as solitary individuals onto the reef. The behavior of *P. cruentatus* is clearer. Being far less abundant than *Myripristis*, individuals of *P. cruentatus* are seen arriving in discrete schools, swimming high above the reef. These schools were especially apparent when an arrival point for the species was discovered at Honaunau, at a location near a coral cave midway down a steep slope. The crest of the slope is in water 12 m deep, the base is about 35 m deep, and the cave is at a depth of about 20 m. On six mornings, I witnessed the arrival here of a large school of *P. cruentatus* (Figure 7). Although a few early arrivals had already been in the area for as long as 10 min, the sudden appearance of the school, containing 30 to 50 fish, was a readily recognized event. After arriving together, many of these fish remained as a unit, milling close to the substrate just outside the entrance to the cave; however, many others of the group dispersed along the face of the slope, where much cover is available under overhanging coral growths. After about 10 min, during which these fish hovered close to the coral, all gradually took shelter: the majority entered the cave, whereas others, either as individuals or groups of a few fish, found cover in the varied crevices and smaller caves along the face of the slope. On the two occasions when the time was noted, the last of these fish were seen entering shelter at 29 and 32 min before sunrise, respectively.

After the initial upsurge in their numbers on the reef, some *Myripristis* go under cover right away, but most continue to swim above the coral for 10 min or so. On eight mornings I noted when the last of these had entered their caves (Figure 7).

Cover-Seeking of Other Nocturnal Fishes

About the time that *Priacanthus cruentatus* and *Myripristis* spp. are reappearing on the reef in large numbers, members of at least most of the other, less conspicuous nocturnal species are still active close to the substrate. It remains uncertain just when, in response to the approaching dawn, many nocturnal fishes cease to range into exposed positions. *Holotrachys lima, Dendrochirus brachypterus, Pterois sphex, Scorpaena coniorta, Brotula multibarbata,* and others are among the species that are seen only irregularly during the night, partly because they are not especially numerous. The behavior of the more numerous squirrelfishes of the genus *Holocentrus* is less obscure. Individuals of any one

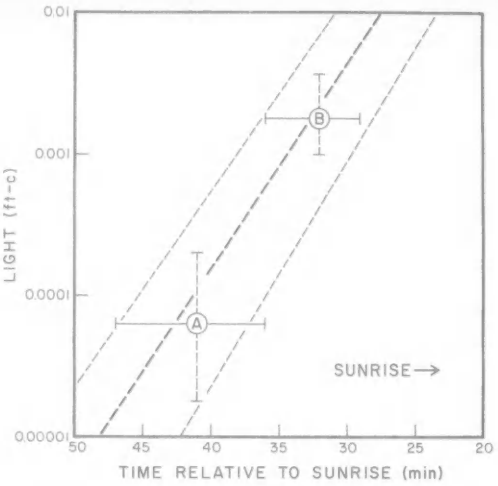

FIGURE 7.—Some characteristics of certain nocturnal fishes during morning twilight. A. *Priacanthus cruentatus*: when a certain school returned to the reef on six mornings. B. *Myripristis* spp. when the last individual descended to the reef on eight mornings. For explanation of symbols, see legends for Figures 2, 4, and 5, except that this figure represents morning events.

species of *Holocentrus* do not go under cover at about the same time, as is true for *Myripristis* spp. Instead, their numbers gradually diminish over a period of about 20 min during early twilight, approximately 50 to 30 min before sunrise. By the time holocentrids of the genus *Myripristis* have gone under cover, about 30 min before sunrise, the only nocturnal fishes consistently in view are scattered individuals of *Holocentrus sammara*, *Apogon menesemus*, and *A. snyderi*. At this point the morning interim period has begun.

THE MORNING INTERIM PERIOD

As the midwaters are being vacated by the species of *Myripristis*, it is getting light enough for the human observer to visually distinguish details of the reef around him. It is about 30 min before sunrise, and relatively few fishes are seen. Scattered individuals of several nocturnal species, especially *Holocentrus sammara*, *Apogon menesemus*, and *A. snyderi*, still hover in view close among the coral but are not active. Among diurnal fishes, a number of chaetodontids, many paired, move about close among the coral; the nocturnal colorations of many are just now giving way to their diurnal hues. Despite these active fishes, the overall aspect on the reef is quiet. Thus, the morning interim, like the evening interim, is termed the "quiet period."

About 5 min into the interim, or quiet, period, when sunrise is still about 25 min away, and when the last *Holocentrus sammara* is now under shelter, the first strong indications of increasing activity in diurnal fishes is seen. At this time the large and medium-sized surgeonfishes begin to assemble in depressions between the towering heads of the coral *Porites*. The timing of this event was recorded on six different mornings (Figure 8). These assemblages, which include

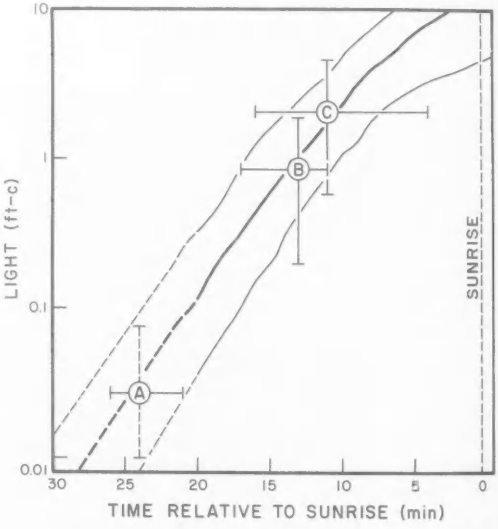

FIGURE 8.—Some characteristics of certain diurnal fishes during morning twilight. A. When species of acanthurids began to assemble in reef depressions on six mornings. B. When diurnal fishes first surged into the water column on nine mornings. C. When the first scarid appeared away from cover on nine mornings. For explanation of symbols, see legends for Figures 2, 4, and 5, except that this figure represents morning events.

Acanthurus achilles and *A. leucopareius*, continue to develop for about 5 min. *Zanclus canescens* soon joins in, swimming in groups of four to six, as do various chaetodontids, most notably the many species of *Chaetodon*. These become increasingly active, while at the same time staying close to the substrate. Pomacentrids, including *Pomacentrus jenkinsi* and *Plectroglyphidodon johnstonianus*, have become noticeably active close to the coral and rocks. The chaetodontid *Centropyge potteri* becomes active in the same area, and joins the pomacentrids in feeding on benthic organisms at this time. In this benthic activity, these fishes swim among the stragglers of *Apogon snyderi* and *A. menesemus*, which are now gradually going under cover.

At about 20 min before sunrise the assemblages that have been developing in depressions among the towering corals begin to rise out of the depressions and range over the reef. At first they stay close to the substrate, but then, in an action comparable in abruptness to their vacating the water column in the evening, these diurnal fishes rise 1 to 2 m above the reef. This event marks the end of the morning interim period.

THE MASS EMERGENCE OF DIURNAL FISHES

Twilight Upsurge in Activity and Reoccupation of the Water Column

The sudden surge of diurnal fishes into the water column was noted on nine mornings (Figure 8). Surgeonfishes, and to a lesser extent parrotfishes, are the predominant forms here, just as they are during the increased activity during evening twilight. As in the evening, they swim in aggregations that move back and forth 1 to 3 m over the reef, or in schools that move with seeming purpose from one location on the reef to another.

The milling assemblages.—The assemblages that develop above the reef in the morning are more segregated by species than are those that occur in these same locations during the evening. The initial surge of activity into the water column 10 to 15 min before sunrise involves mostly medium to larger herbivorous species, including surgeonfishes *Acanthurus achilles*, *A. leucopareius*, and *Naso lituratus*. These do not show any purposeful direction; rather, they mill about over a defined part of the reef. Also swimming in and around these assemblages are a number of larger diurnal fishes that occur as individuals, or groups of two or three fish: these include the filefish *Cantherines dumerili*, the triggerfishes *Sufflamen bursa* and *Melichthys niger*, and the parrotfishes *Scarus perspicillatus* and *S. rubroviolaceus*.

The time that the first parrotfish was seen was noted on nine different mornings (Figure 8). This observation included all species, yet *S. perspicillatus* or *S. rubroviolaceus*, the two largest species, were seen first in five of the nine instances, despite their being by far the least numerous species of the genus *Scarus*. The smaller, but much more numerous *Scarus* species, *S. sordidus*, *S. dubius*, and *S. taeniurus*, generally appeared later. During the time that the smaller parrotfishes are appearing, the remnants of numerous mucous envelopes, in which many of them had spent the night (see, for example, Winn, 1955; Casimir, 1971), drift about close to the substrate.

The twilight migrations.—Just as they do during evening twilight, many species migrate from one location on the reef to another at this time. As in the evening, they travel in schools that frequently are drawn out as long processions. Again, specific routes are followed morning after morning, indicating that well-defined patterns exist. Although these patterns remain obscure for most participants, some individuals clearly reverse their evening direction. Thus, having spent the night sheltered on the shallower parts of the reef, many individuals of the plankton-feeding surgeonfish *Naso hexacanthus*, along with many of the damselfish *Chromis verater*, return to their deeper water feeding grounds high above the offshore edge of the reef. As mentioned above, this pattern is obscured by the many other individuals of these species that do not migrate inshore at nightfall, but instead spend the night sheltered on the deeper parts of

the reef, directly below their midwater feeding grounds.

Just as they do in the evening, many smaller herbivores, including the surgeonfishes *Zebrasoma flavescens* and *Ctenochaetus strigosus*, as well as the parrotfish *Scarus sordidus*, migrate from one area to another, but the patterns are not yet defined. Again, the picture is obscured by the many other individuals of these same species throughout the study areas that do not join these migrations. Thus, as in the evening, it remains unknown just what sort of redistribution most of these fishes achieve. Nevertheless, the patterns seem to relate to the transition toward the diurnal situation.

Ascent of the Plankton-Feeding Damselfishes

Adults of the larger plankton-feeding damselfishes, *Abudefduf abdominalis*, *Chromis ovalis*, *C. verater*, and *Dascyllus albisella*, join the surge of diurnal fishes that rise into the water column 10 to 15 min before sunrise. Because they all ascend above the reef at about the same rate, the most readily observed, *D. albisella*, is representative. On five mornings, stationed in one location where the water was 8 m deep, I noted when a particular aggregation of *D. albisella* was clear of cover, and then as it gradually ascended into the water column, I estimated when it had attained levels of 3 m, and (on three mornings) 5 m above the reef (Figure 9).

The smaller plankton-feeding damselfishes *Chromis leucurus* and *C. vanderbilti* rise above the reef later than do these larger species. On nine mornings, at a variety of locations, I noted when the first individual of *C. leucurus* moved out away from shelter (Figure 10). These fish remained in about this position, solitary and with shelter close at hand, for some time; at 15 min after sunrise they had moved a little farther from shelter, but otherwise their position was unchanged. *C. vanderbilti* follows an even later schedule. On the one occasion that it was recorded, solitary individuals first appeared close to shelter at 1 min after sunrise, and 11 min later had just begun to aggregate in pockets among the rocks.

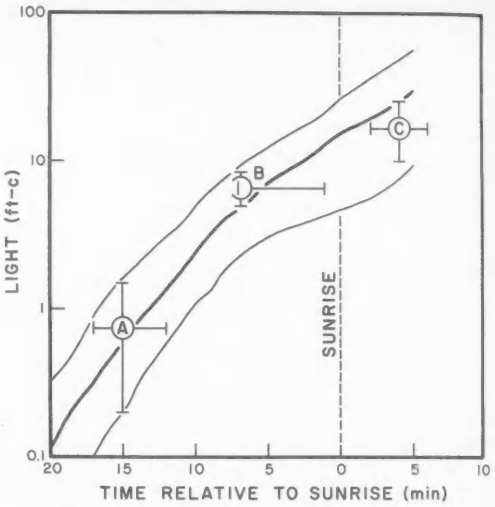

FIGURE 9.—Ascent of an aggregation of *Dascyllus albisella* into the water column during morning twilight. A. When the aggregation was first clear of cover above the reef on five mornings. B. When the aggregation had risen to 3 m above the reef on five mornings. C. When the aggregation had risen to 5 m above the reef on three mornings. For explanation of symbols, see legends for Figures 2 and 4, except that this figure represents morning events.

Emergence of Other Diurnal Fishes

Throughout the time that the diurnal fishes noted above are resuming activity on the reef, the many sedentary diurnal fishes become increasingly evident, including the hawkfishes *Paracirrhites forsteri*, *P. arcatus*, and *Cirrhitops fasciatus* and also the blennies *Exallias brevis* and *Cirripectus variolosus*. These begin moving out from shelter during the interim period, but so unobtrusively that their initial appearance usually goes unnoticed.

When the milling assemblages and migrating schools dominate the scene, additional fishes become active close among the rocks and corals, including the triggerfishes *Sufflamen bursa* and *Rhinecanthus rectangulus*, as well as the filefishes *Cantherines sandwichiensis* and *Pervagor spilosoma*. These too, being scattered and relatively inconspicuous, often go unnoticed at first appearance.

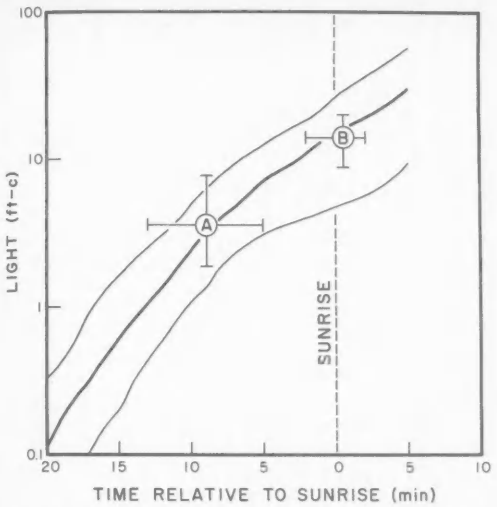

FIGURE 10.—Some characteristics of certain diurnal fishes during morning twilight. A. *Chromis leucurus*: when the first individual left cover on nine mornings. B. *Acanthurus nigrofuscus*: when individuals first appeared in school above the reef on three mornings. For explanation of symbols, see legend for Figure 2, except that this figure represents morning events.

Late Risers

Observations on Acanthurus nigrofuscus.—The assemblages of larger and medium-sized surgeonfishes that have been swimming above the reef since the initial upsurge in activity, begin to break up about the time of sunrise. Initially these aggregations become less active, then dissolve into smaller, discrete groups, now closer to the sea floor, that increasingly range out over the reef. Soon they assume activity typical of daylight. At about the time that these aggregations are breaking up, the small surgeonfish *Acanthurus nigrofuscus* makes its first appearance. Soon after, individuals of this species assemble in large schools over the reef and proceed to follow a course of action much like that taken earlier by their larger relatives. The initial appearance of *A. nigrofuscus* in a school above the reef was noted on three occasions (Figure 10). They maintain these large, active schools, as did the large species, for about 20 min, when finally these schools too dissolve into smaller discrete groups that range out over the reef.

Observations on Thalassoma duperrey.—As is true in the Gulf of California (Hobson, 1965, 1968), the smaller labrids are among the last diurnal fishes to become active in the morning. The initial appearance of the ubiquitous *Thalassoma duperrey* in the morning is representative of this group, just as is its cover-seeking in the evening. It is much easier to recognize the first individual to appear in the morning than the last individual to take cover in the evening, and on 16 mornings I noted the first *T. duperrey* to become active in my immediate surroundings (Figure 11). These fish are often unmistakable when they are just resuming activity; for several seconds after emerging from their resting places many "yawn," opening the mouth wide, and "stretch," drawing their body into various contortions.

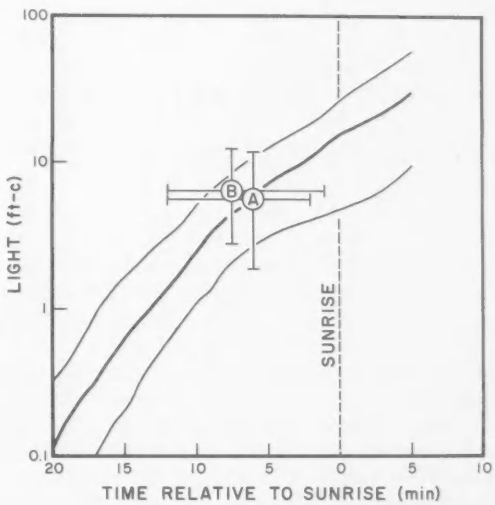

FIGURE 11.—Some characteristics of certain labrids during morning twilight. A. *Thalassoma duperrey*: when the first individual left cover on 16 mornings. B. *Labroides phthirophagus*: when the first individual left cover on nine mornings. For explanation of symbols, see legend for Figure 2, except that this figure represents morning events.

Observations on Labroides phthirophagus.—In describing evening cover-seeking by *Labroides phthirophagus* above, data are presented on just one individual. At least five individuals of this species are involved in the nine observations of the initial morning appearance (Figure 11).

Other fishes seeking cleaning from this species often hover in typical soliciting fashion at the cleaning stations (see Losey, 1971) for some time before the cleaners have made their initial morning appearance.

SUMMARY

The data presented above are summarized in Figures 12 and 13.

DISCUSSION

Most fishes on the reefs at Kona behave differently in daylight than they do at night, and during twilight their actions express a transition between these two modes of behavior. In essence, we are concerned with predominantly diurnal or nocturnal fishes changing from active to relatively inactive states, or the reverse, and the influence that certain characteristics of twilight itself have on these actions. These considerations underlie the following discussion.

FEEDING LOCATIONS VERSUS SHELTER LOCATIONS

The daily activities of tropical reef fishes show the overriding influence of two primary concerns: to eat and to avoid being eaten. Reef fishes must contend with predators at all times, but during those periods of day when they are active their actions seem dominated by their own feeding. On the other hand, during those periods of the day when they are relatively inactive, resting, their major consideration seems to be security. Thus, for example, the small parrotfish *Scarus taeniurus* grazes in exposed positions during daylight, but rests in coral crevices at night, often encased in a mucous envelope. Winn and Bardach (1959) discussed the function of the mucous envelope as a defense against nocturnal predators.

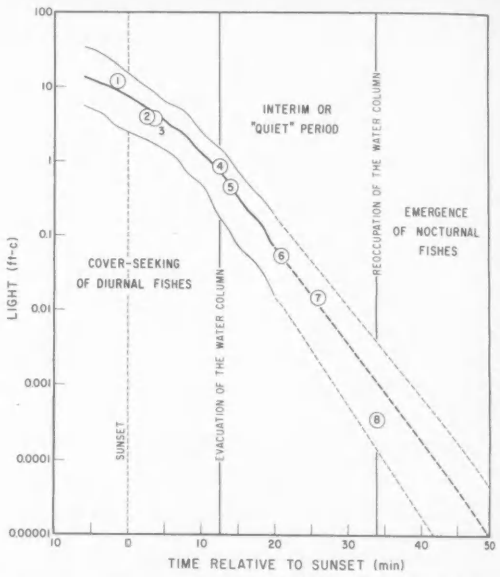

FIGURE 12.—Summary of events during the evening transition period. For explanation of symbols, see legends for Figures 2, 4, and 5. In addition, numbered points represent mean values for events. 1) When the last *Thalassoma duperrey* took cover on five evenings. 2) When a certain *Labroides phthirophagus* took cover on five evenings. 3) When the last *Chromis leucurus* took cover on three evenings. 4) Abrupt vacating of water column by diurnal fishes; the beginning of the interim, or "quiet," period: 12 evenings. 5) When *Apogon snyderi* first left cover on four evenings. 6) When *Apogon menesemus* first left cover on five evenings. 7) When *Holocentrus sammara* first left cover on four evenings. 8) When *Myripristis* spp. abruptly appeared in large numbers above the reef; the end of the interim, or "quiet," period: eight evenings.

Tropical reef fishes exhibit either one of two general means of reducing predation during their inactive periods: they school or they seek cover (Hobson, 1968). Thus, many fishes that forage at night, including various clupeids, pomadasyds, mullids, lutjanids, and carangids, characteristically spend the day in large inactive schools that hover in exposed positions on or near the reef. The advantage of such schools in reducing predation was discussed earlier (Hobson, 1968). Significantly, no diurnal fish is known

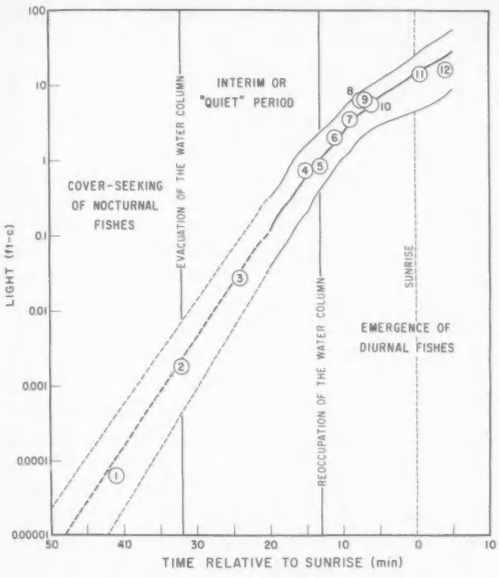

FIGURE 13.—Summary of events during the morning transition period. For explanation of symbols, see legends for Figures 2, 4, and 5, except that this figure represents morning events; in addition numbered points represent mean values for events. 1) When a particular school of *Priacanthus cruentatus* returned to the reef on six mornings. 2) When last *Myripristis* spp. took cover on reef; the beginning of the interim, or "quiet," period: eight mornings. 3) When acanthurids began assembling in depressions in the reef on six mornings. 4) When an aggregation of *Dascyllus albisella* in a particular location had moved away from cover, above the reef, on five mornings. 5) When diurnal fishes first surged 1 to 2 m into the water column; end of the interim, or "quiet," period: nine mornings. 6) When the first scarid appeared away from cover on nine mornings. 7) When the aggregation of *Dascyllus albisella* (see #4), had risen 3 m above the reef on five mornings. 8) When *Chromis leucurus* first left cover on nine mornings. 9) When *Labroides phthirophagus* first left cover on nine mornings. 10) When *Thalassoma duperrey* first left cover on 16 mornings. 11) When *Acanthurus nigrofuscus* first appeared in school above the reef on three mornings. 12) When the aggregation of *Dascyllus albisella* (see #4 and #7) was 5 m above the reef on three mornings.

to similarly school during its nocturnal inactive period. Fishes that form large schools in exposed locations when inactive are not well represented on Kona reefs; possible reasons are given below. The other means of attaining security while inactive—seeking shelter under rocks or coral—is characteristic of many diurnal as well as nocturnal fishes, including labrids, scarids, balistids, holocentrids, and apogonids. This second tactic is employed by most reef fishes in Kona. The advantage of cover in reducing predation is obvious. Some of the nocturnal fishes, for example, species of *Myripristis* and *Holocentrus*, as well as *Priacanthus cruentatus*, characteristically aggregate under cover on the reef in daylight; in contrast, none of the diurnal species were noted to aggregate when sheltered in their nocturnal resting spots.

Each of the wide variety of fishes on the Kona reef has its own specific feeding habits (Hobson, in preparation), and these relate in large part to where each is active. A suitable feeding location for any given species may or may not be near areas that offer it suitable security during its inactive period. Consequently, the major actions of these fishes characteristic of twilight relate to moving between feeding locations and shelter locations.

TWILIGHT REDISTRIBUTION

Most of the readily observed movements of Kona reef fishes during twilight fit within a framework of three broad, overlapping categories: 1) individuals of some species migrate extensively between offshore feeding grounds and shelter locations on the reef; 2) other species migrate from one part of the reef to another; and 3) still others make short but well-defined vertical migrations between plankton-feeding locations in the water column and shelter locations on the reef below. These movements are all performed by fishes swimming in groups. The movements of most reef fishes, which remain poorly known, do not seem referable to any of these categories; nevertheless, limited evidence indicates that at least many of them follow well-defined patterns of some sort. There is much overlap between the different categories and the activity of many species comprise elements of more than one type. It is for convenience in

presentation that each category is discussed separately below.

Offshore Migrations

Nocturnal fishes.—In many seas, certain reef fishes are known to make extensive feeding migrations away from the reef at nightfall; outstanding examples include certain clupeids, pomadasyids, carangids, and other schooling fishes in the Gulf of California (Hobson, 1965, 1968) and tropical Atlantic (Starck and Davis, 1966). These migrations are best known among those nocturnal predators that school on or near the reef during their inactive periods. Although such schooling fishes and their offshore migrations during twilight are a major characteristic of some areas, they are not prominent on Kona reefs. This is understandable. The reefs where these schooling fishes and their offshore migrations are so pronounced in the Gulf of California and in the tropical Atlantic are surrounded by extensive open sand flats or grass beds. These vast stretches are nocturnal feeding grounds of the fishes that migrate away from the reefs. The importance of proximate feeding grounds of this sort to such fishes is well known (Longley and Hildebrand, 1941; Randall, 1963; Hobson, 1968). Similar feeding grounds do not surround Kona reefs, which are instead bordered by a precipitious drop into deep water. Not surprisingly, the relatively few species that migrate offshore at nightfall from Kona reefs, including *Priacanthus cruentatus* and *Myripristis* spp., seek open-water prey. Furthermore, whereas fishes migrating over the extensive sand flats and grass beds adjacent to reefs elsewhere often travel considerable distances (Starck and Davis, 1966; Hobson, 1968), comparable data are not available for *Priacanthus* and *Myripristis*. It is possible that these fishes do not go much beyond the outer edge of the reef, an area known to be a rich feeding ground for diurnal plankton-feeding fishes (see below).

Diurnal fishes.—Offshore feeding migrations comparable to those made by nocturnal fishes have not been reported for diurnal fishes. In the Gulf of California, the exodus of fishes away from the reef during twilight, transforming the stretches of open sand offshore into centers of activity, is strictly a nocturnal phenomenon; there is no diurnal equivalent, as these open expanses are comparatively without active fishes in daylight (Hobson, 1968).

In Kona, several diurnal fishes, including some individuals of the surgeonfish *Naso hexacanthus* and the damselfish *Chromis verater*, migrate to the offshore edge of the reef during morning twilight. They swim to where the seaward reef-face drops abruptly to great depths and here become part of a large assemblage of plankton-feeding fishes. Apparently plankton is exceptionally rich in this area. The migrations seem to terminate here, but the larger *Naso hexacanthus*, and perhaps other species, periodically range farther offshore during the day. During evening twilight many individuals of these species return inshore to the shallower parts of the reef, a pattern obscured by the many other individuals of these species that shelter themselves on the offshore parts of the reef, below their midwater feeding grounds. It may be that there is not enough suitable cover here to accommodate all of the many fishes that concentrate to feed in this location. This would account for the fact that while some shelter themselves here, others migrate from other areas.

Intrareef Migrations

Conspicuous elements of the transition period are the long drawn-out processions that migrate from one point on the reef to another, following the same routes day after day. Although the redistribution pattern achieved by these movements remains undefined, the phenomenon seems limited to herbivorous fishes, especially the small to medium-sized acanthurids and scarids, and to some plankton feeders. Herbivorous reef fishes are widely reported to be strictly diurnal (Hobson, 1965, 1968; Starck and Davis, 1966). The migratory patterns shown by these fishes are obscured by the many other individuals of the migrating species that do not join these movements.

Some herbivorous species, for example certain parrotfishes (see Bardach, 1958), range far

across the reef in schools while grazing on benthic algae during the day. The intrareef migrations during evening twilight of such fishes may be a return from such excursions to established resting areas at day's end.

Vertical Migrations

The movements discussed so far involve fishes that traverse considerable distances. Many other fishes, some diurnal, others nocturnal, move between feeding grounds and shelter locations in a well-defined pattern that covers no more than a few meters. These are the many plankton feeders that forage in the water column, and find shelter on the reef directly below. Some species, like the diurnal *Naso hexacanthus* and the nocturnal *Myripristis argyromus*, both discussed above, undertake such vertical movements but also make extensive lateral excursions across the reef and beyond. Nevertheless, many plankton feeders, especially smaller species like *Dascyllus albisella*, restrict their activity to a limited area on the reef. Restricted though these movements may be, they follow patterns as well defined as any of those discussed above.

These plankton feeders are either diurnal or nocturnal. Without overlap, those feeding in daylight are inactive after dark, and those feeding at night are inactive in daylight. The respective feeding periods of the two groups are separated by the 15 to 20 min interim, or quiet, period. I noted a similar absence of overlap between diurnal and nocturnal plankton feeders in the Gulf of California (Hobson, 1968), as did Starck and Davis (1966) in the tropical Atlantic. Obviously conditions of plankton feeding differ between day and night. Emery (1968) reported that the composition of plankton over Florida reefs differs between day and night, and I found the same true in Kona (Hobson, in preparation).

Twilight Movements of Other Reef Fishes

The patterns of movement described above are readily recognized because each involves many individual fish moving together. Most reef fishes do not operate in large assemblages but instead are active solitarily or in small groups. Unifying patterns in such species are difficult to recognize, because many discrete units are simultaneously behaving independently at different points on the reef. Nevertheless, limited data show that patterns do exist. Probably the movements of some fall into the broad categories outlined above, but the actions of others, once recognized, probably would represent additional categories. Chaetodontids, labrids, pomacentrids, scarids, balistids, and other diurnal species, as well as many holocentrids, apogonids, scorpaenids, and other nocturnal fishes, all display distinctive nocturnal and diurnal habits. The twilight activities of most of these fishes do not include extensive movements; most change from an active to a relatively inactive state, or the reverse, within a limited area on the reef. Data presented in this report show well-defined temporal patterns in their seeking and everging from cover. Limited additional data indicate that in at least many of these fishes the patterns also have a strong spatial element: consider, for example, the circumstance that at least some individuals of *Thalassoma duperrey* and other species occupy specific resting spots at nightfall.

PATTERNS OF TWILIGHT ACTIVITY

I have developed the thesis that activity of most Kona reef fishes during twilight relates to a transition between diurnal and nocturnal modes of behavior. If these fishes were concerned only with shifting from one mode of behavior to another, the timing of the various transition events could well as not be random. In fact, however, the transition events proceed in an established, well-defined sequence, with characteristics indicating that some force exerts a strong controlling influence. The general pattern has been outlined above (Figures 12 and 13). Some additional characteristics of the transition events warrant discussion.

Fish Size as Expressed in Transition Activity

The time during the transition at which a given fish joins certain of the activities is related to that fish's size. During evening twilight

some of the transition activities are performed by the smaller fishes first. Thus, for example, the increased tendency of many fishes to aggregate, as seen especially in acanthurids and scarids, occurs first in the smallest species of the respective groups: *Acanthurus nigrofuscus* among the acanthurids, and *Scarus taeniurus* among the scarids. Consider too the plankton-feeding damselfishes, which during the transition period progressively descend closer to the sea floor and finally take cover on the reef. The smallest species, *Chromis vanderbilti*, is first to seek cover, and the next smallest, *C. leucurus*, is second. The other, larger damselfish species follow later. Similarly, the smallest of the surgeonfishes, *Acanthurus nigrofuscus*, is the first of that family to go under cover, and the others follow in order roughly corresponding to increasing size. Most acanthurids on the reef are of about the same size and therefore show similar timing in seeking cover; nevertheless, the larger species, like *A. dussumieri*, are the last to settle down. The same pattern occurs among the filefishes, where the smaller *Cantherines sandwichiensis* takes cover long before the larger *C. dumerili;* and among the parrotfishes, where the smallest, *Scarus taeniurus*, is no longer seen when such larger relatives as *S. rubroviolaceus* and *S. perspicillatus* are still active. The effect operates within species, just as it does between species; thus, for example, large adults of *Scarus rubroviolaceus* are still active long after all the small juveniles of this species have gone under cover.

In the morning the situation in these same species is reversed. The larger individuals are the first of the diurnal fishes to emerge from cover, and the others appear in order roughly according to decreasing size to perform their characteristic transition activity.

It remains uncertain to what extent fish size relates to the transition activity of nocturnal fishes. *Holocentrus sammara*, *Apogon menesemus*, and *A. snyderi*, which are consistently the first nocturnal species to leave shelter in the evening and the last to seek shelter in the morning, are the largest of their respective groups common in Kona; however, additional data are lacking.

Increased Activity During Twilight

One senses a marked increase in activity among fishes at two times during the twilight periods: in the evening, from just before sunset to about the time that the diurnal fishes abandon the water column, and in the morning, from the time the diurnal fishes reoccupy the water column to just after sunrise. This impression of heightened activity derives mostly from a combination of the following: 1) fishes migrating from one location to another; 2) increased territorial aggression (evening only); and 3) an increased tendency to aggregate in locations more visible to the observer.

Migrations.—The migrations are discussed above. Their contribution to a general impression of increased activity is obvious.

Territorial aggression.—A minor element of the increased activity during evening twilight is increased territorial aggression. During the day there are frequent territorial disputes among many of these fishes, often, if not generally, relating to feeding areas; this is a frequent source of conflict among the acanthurids (see, for example, Jones, 1968). Aggression during evening twilight, which was noted only in diurnal fishes, seems unrelated to feeding; rather, it may express conflict over resting spots. It is significant not so much that such aggression occurs, but that there is so little of it. With such a vast number of fishes settling into resting positions on the reef at nightfall, one might expect individuals with similar requirements to compete strongly for optimum spots. That relatively little aggression of this sort occurs suggests that some mechanism establishes spatial distribution without overt conflict. One possibility is that each individual has a well-established resting spot; this is suggested by the two individual *Thalassoma duperrey* that were observed to be strongly attached to particular locations. However, this hypothesis is not widely supported. Overall, I recognized only a relatively few cases where what seemed to be the same individual returned to a particuar spot on

a number of different nights, and even these did not seem to have a long-standing attachment to such locations. More important, I was unable to recognize attachments to particular locations in most of the diurnal species that occupy resting spots when inactive. There are scattered reports of reef fishes returning to established resting spots: Winn and Bardach (1960), for example, noted that a certain species of parrotfish in Bermuda has "home caves," and Starck and Davis (1966) suspected the same to be true of two parrotfish species in Florida. Nevertheless, pending accumulation of additional data from a variety of fish groups the question on a broad scale remains unresolved.

Nocturnal fishes seeking cover in the morning were not seen in conflict over resting spots. A major general behavioral difference between diurnal and nocturnal fishes may account for this. Unlike diurnal fishes, which generally are solitary in their resting places, many nocturnal species, including *Myripristis* spp., *Holocentrus* spp., and *Priacanthus cruentatus*, aggregate in their daytime shelters.

Increased tendency to aggregate in locations more visible to the observer.—The general impression of increased activity during the periods of twilight defined above stems mainly from the many diurnal fishes that congregate one to several meters above certain parts of the reef at these times. These fishes, which concentrate over areas where at least most of them seek shelter, mill about actively, but without recognized direction. Although surgeonfishes predominate in these aggregations, species from many families of diurnal fishes are represented. However, it can be questioned whether or not this phenomenon does in fact involve increased activity. At least to some extent the fishes only appear to be more active. At this time, compared to other times of day, they are more concentrated and swim in locations that are more visible to the observer. Mostly these are gregarious species, but the groups in which they swim during midday are less visible than the twilight assemblages, being smaller, more loosely organized, and occurring closer to the substrate at many different places on the reef.

THE INFLUENCE OF PREDATORS ON TWILIGHT ACTIVITY

I have emphasized that the twilight activity in reef fishes proceeds in an established, well-defined sequence. Now I suggest that this well-ordered series of events is shaped by the threat of crepuscular predators.

In the Gulf of California (Hobson, 1965, 1968) and certain parts of the tropical Atlantic (Starck and Davis, 1966), large piscivorous fishes are primarily crepuscular. The increased vulnerability of smaller free-swimming fishes during twilight, especially those in schools, has been discussed (Hobson, 1968). Mechanisms that reduce the threat from predators during daylight and darkness apparently are less effective during the transition between these two major segments of the diel cycle. Thus attacks by large piscivores on schooling clupeids, pomadasyids, and small carangids in the Gulf of California become increasingly frequent at about the time of sunset, and peak about 20 min later. After peaking, the predation ceases, and the piscivores withdraw. Most of the schooling prey, which are nocturnal predators, then migrate to their offshore feeding grounds (Hobson, 1968). Because this activity is a dominant feature of the reef situation in the Gulf of California, one can relate it to the concurrent actions there of such smaller nonschooling fishes as labrids, pomacentrids, chaetodontids, acanthurids, and balistids. The pattern of cover-seeking in these fishes, and the subsequent emergence of such nocturnal forms as holocentrids and apogonids, follows much the same pattern in the Gulf as that of their close relatives in Kona, described in this report. Observations on the transition events in the Gulf of California were not detailed to the extent of those in Kona; nevertheless, many of the same phenomena were reported from the Gulf. For example, referring to evening observations I pointed out that labrids are among the first of the diurnal fishes there to seek cover and that the emerging *Apogon* mix with some of the diurnal fishes close among the rocks as the latter are taking cover (Hobson, 1965, 1968). I am confident that the techniques used in Kona, if

repeated in the Gulf of California, would generate data much like those presented in this report. Although the faunas of the two areas have only a few species in common, there are many generic parallels. Genera common to both areas include: *Bodianus, Thalassoma, Halichoeres,* and *Hemipteronotus* (labrids); *Abudefduf, Chromis,* and *Pomacentrus* (pomacentrids); *Chaetodon* and *Holacanthus* (chaetodontids); *Acanthurus* (acanthurids); *Balistes* and *Sufflamen* (balistids); *Holocentrus* and *Myripristis* (holocentrids); *Apogon* (apogonids); and many others. Congeners from these two widely separated areas behave similarly.

In the Gulf, one can readily relate the distances small fishes are from shelter at different times during the transition period with the concurrent attacks by large piscivores on the schooling fishes; when this piscivorous activity peaks, most of the small nonschooling fishes are under cover. As I pointed out (Hobson, 1968, p. 84), ". . . during those periods of morning and evening twilight, when schooling fishes are most heavily exploited, neither diurnal nor nocturnal plankton feeders (mostly *Chromis, Abudefduf, Myripristis* and *Apogon*) are in midwater."

Significantly, the reef fishes in Kona all are close to shelter at the time, relative to sunrise or sunset, that schooling fishes in the Gulf of California are under heaviest attack (Figures [3]14 and '15). At the same time that predation upsurges in the Gulf, the water column is vacated in Kona, both by nocturnal fishes during early morning twilight and by diurnal fishes during early evening twilight. Furthermore, the water column is not then reoccupied in Kona, either

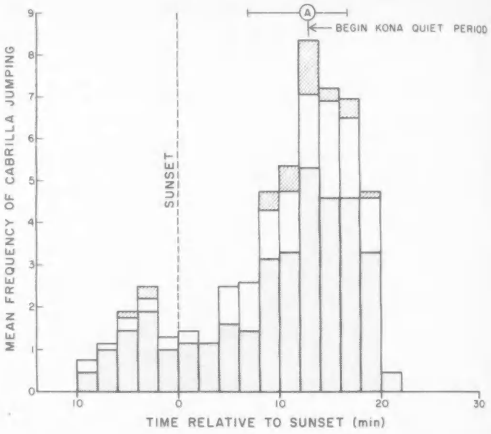

FIGURE 14.—Time of peak predation (*Mycteroperca rosacea* when preying on schooling *Harengula thrissina*) in the Gulf of California relative to the evening interim, or "quiet," period in Kona. Duration of twilight is similar in the two areas as the difference in latitude is only about 4°. Stippled area of the bars represents the frequency of attacks involving one *M. rosacea*; white area of bars, the frequency of attacks involving two to seven *M. rosacea;* hatched areas of bars, the frequency of attacks involving eight or more *M. rosacea* charging simultaneously. Also plotted is the mean (A) and the range of times, relative to sunset, that diurnal fishes vacated the water column in Kona. (For further information regarding this figure, see text footnote 3.)

[3] When preying on schooling flatiron herring, *Harengula thrissina,* in shallow water in the Gulf of California, the cabrilla, *Mycteroperca rosacea* attacks from below. Its charge carries the cabrilla up through the herring school and momentarily out of the water (see Hobson, 1968). Because the herring schools are close to the beach throughout the day and into twilight, an observer on the beach can obtain an index of predatory activity by noting the incidence of attacks—seen as cabrilla jumping out of the water amid the herring. These data were collected on seven consecutive evenings and were presented earlier (Hobson, 1968, Figure 18).

In Figure 14, I have pooled these data, and present the mean values in time relative to sunset (when presented in Hobson (1968) these data were broken down by days, and shown against time of day). The graph also reflects the fact that discrete attacks involve varying numbers of cabrilla charging simultaneously. Unfortunately, the attacks by cabrilla on herring do not provide an index of predation beyond about 20 min after sunset; at this time, with the cabrilla and other predators still highly active, the herring migrated offshore. Thus the sudden drop in attacks shown in the figure reflects the herring's departure, not a decline in predation. The predators continued to attack other schooling fishes in the area, mostly pomadasyids, for a short while longer, and these prey schools did not leave the inshore waters until the predators had withdrawn (Hobson, 1968). In any event, because the attacks by cabrilla on herring provided an index only for the initial upsurge in predatory activity, it is meaningless to relate these data to the latter stages of the Kona quiet period.

[4] Data on predation by cabrilla on flatiron herring were collected on three consecutive mornings (see Hobson, 1968). Unlike the evening situation in the Gulf of California, where the herring leave the inshore waters while the cabrilla and other predators are still highly active, in the morning the herring arrive inshore before the predators have begun feeding. Therefore, the attacks by cabrilla on flatiron herring in the morning provide an index of predatory activity spanning all of the twilight period, and thus can be related to the entire interim, or "quiet," period in Kona.

by diurnal fishes during morning twilight, or by nocturnal fishes during evening twilight, until after the time that predation in the Gulf has subsided. Thus, the time of maximum predation in the Gulf is equivalent to what is aptly called the "quiet" period in Kona. Obviously the term "quiet" would be a misnomer if applied to this part of the transition period in certain parts of the Gulf, it being the time when the schooling fishes are under heaviest attack. These schooling species, for example the herring *Harengula*, cannot take shelter under rocks or coral on the reef, as have the other smaller fishes, and thus are exposed to predators during a time when they seem to be especially vulnerable. The disadvantage of schooling fishes at this time, as compared to other potential prey of the piscivores, was pointed out earlier (Hobson, 1968). Thus, if there is an advantage in being close to shelter when predators are most effective, the actions of Kona reef fishes during twilight are adaptive to any increased threat from predators that might exist at that time.

Other behavioral characteristics of Kona reef fishes during the day-night transition period can be interpreted as mechanisms to reduce predation. If one accepts the premise that smaller fishes are more vulnerable to predation than larger ones, it is significant that smaller individuals seek cover earlier in the evening, when danger from predators apparently is progressively intensifying. The same significance can be attributed to their leaving cover later in the morning when danger from predators apparently is progressively diminishing. Consider too the increased tendency to aggregate among so many fishes that just mill over a given section of the reef. Although this behavior probably has other functions as well, it may also contribute some measure of security from predators. It was pointed out earlier (Hobson, 1968) that fishes in such aggregations attain the same protection from predators as do those in schools (if one wishes to distinguish between such assemblages).

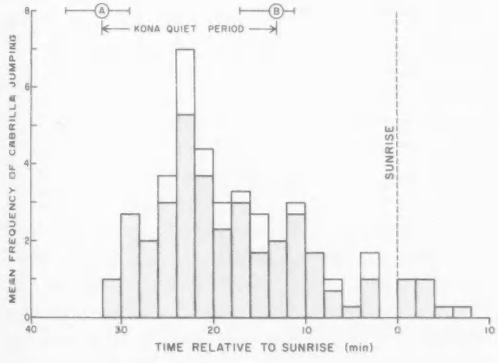

FIGURE 15.—Time of peak predation (*Mycteroperca rosacea* when preying on schooling *Harengula thrissina*) in the Gulf of California relative to the morning interim, or "quiet," period in Kona. For explanation of symbols, see legend for Figure 14. The mean and ranges of both the beginning (A) and end (B) of the Kona quiet period, defined by events described at length in this report, are plotted. (For further information regarding this figure, see text footnote 4.)

Clearly the overall pattern of activity in Kona reef fishes during twilight can be interpreted as being strongly influenced by crepuscular predators. Yet, critics of this hypothesis can point out that an obvious piscivorous threat is absent, at least relatively so when the Kona habitats are compared to those of the Gulf of California.

Hawaiian reefs have been known to be lacking in some of the major predatory fish-groups that are common on most other tropical Pacific reefs. Most notable among these are the shallow water groupers (Serranidae) and snappers (Lutjanidae)—Gosline and Brock, 1960; Randall and Brock, 1960. There are several large carangid species in Hawaii, but the only one that is numerous in Kona, *Caranx melampygus*, is represented mostly by small individuals. Possibly heavy pressure from fishermen along Hawaiian shores keeps the numbers of large carangids at a low level. Because the major piscivorous fishes on the reef at Kona (aside from some of the moray eels, which probably do not prey significantly on free-swimming fishes) are relatively small, they do not seriously threaten the adults of the species being considered here. These include such predators as *Fistularia petimba*, *Aulostomus chinensis*, *Paracirrhites forsteri*, *Parupeneus chryserydros*, and *Bothus mancus*. The predatory activity of these and other species

is detailed elsewhere (Hobson, in preparation). The occasional occurrence during twilight of large barracuda, *Sphyraena barracuda*, and sharks, especially *Carcharhinus milberti*, would not seem to have much impact on the general behavior patterns of the reef fishes. However, any behavior that reduces vulnerability to predators certainly would enhance survival on the occasions when such predators do appear, and the effect of this circumstance may be greater than is readily apparent. Nevertheless, with neither schooling prey nor the predators that exploit them being major elements of the fauna, the vigorous interactions such fishes so prominently generate during twilight in the Gulf of California are essentially missing in Kona.

The absence of large piscivores on the Kona reef as compared, for example, with the Gulf of California, may bear on the relative scarcity in Kona of prey fishes in large schools. Reason for the relative absence of such fishes in Kona was discussed above. The many schooling prey in the Gulf of California was held to be a major factor in the occurrence there of so many large piscivores (Hobson, 1968). For whatever reason these faunal elements are missing in Kona, the question remains: if the threat from predators strongly influences the well-defined sequence in which fishes in the Gulf seek and leave cover during the day-night transition, how is it that reef fishes in Kona show essentially the same pattern when the threat of large piscivores to them is comparatively mild?

We have been focusing on the situations in Kona and the Gulf of California, when in fact it seems that related fishes on most, if not all, tropical reefs, show similar behavior during twilight. Data are lacking for most areas, so this conclusion remains tentative. Nevertheless, not only do related fishes common to Kona and the Gulf of California behave similarly, as described above, but limited data from other seas, including the tropical Atlantic (Starck and Davis, 1966) show essentially the same pattern. The similar pattern of events in these widely separated areas indicates a long evolution that in any one locality transcends the existing situation, even the existing species.

One would expect predator-prey relations among fishes to have responded similarly throughout time to certain basic, unchanging phenomena. Among others, these phenomena would have included the characteristics of light underwater and the effect of these characteristics on visually feeding predators at different times of the day, as well as the probable difficulties such predators experience in choosing a target from among the many confronting them in a fish school (Allen, 1920a, 1920b; Hobson, 1968; and others). With this common heritage, it would be surprising if behavior patterns relating to predator-prey interactions did not show today deep-rooted parallels on even widely separated reefs. I suggest, therefore, that the behavior of tropical reef fishes during twilight in all seas, including Kona, reflects the impact of a historic threat from predators.

CONCLUSIONS

1. At least most of the reef fishes at Kona, Hawaii, behave differently in daylight than they do at night, and during twilight their actions express a transition between these two modes of behavior. Most of these fishes are either diurnal or nocturnal, with the diurnal species relatively inactive at night and the nocturnal species relatively inactive in daylight.

2. During their period of major activity, the actions of these fishes are dominated by behavior relating to their own feeding, and often this takes them to specific feeding grounds. During their inactive periods their behavior relates strongly to their own security, and usually they take shelter. Consequently, the actions of these fishes during twilight relate primarily to moving between feeding locations and shelter locations.

3. The twilight movements of many of these fishes involve well-defined migrations. A) Some members of certain nocturnal species migrate extensively between shelter locations on the reef and feeding grounds offshore; species in this category include *Myripristis* spp. and *Priacanthus cruentatus*. B) Some members of certain other species migrate between shelter locations on one part of the reef and feeding grounds on another; species in this category are mostly di-

urnal herbivores and plankton feeders, including certain acanthurids, scarids, and pomacentrids. C) Many small plankton-feeding species make short, but well-defined vertical migrations between shelter locations on the reef and feeding locations in the water column directly above; diurnal species in this category include certain pomacentrids and chaetodontids, and nocturnal species include certain apogonids and holocentrids.

4. Activity associated with the transitions from day to night, and from night to day, proceeds in an established, well-defined sequence. Both evening and morning periods of changeover comprise three distinct segments. In the evening, these are: 1) *the shelter-seeking of the diurnal fishes* (from about 30 min before sunset to about 13 min after sunset), which ends when the last group of diurnal fishes still milling above the reef, mostly acanthurids, abruptly descend to cover; 2) *the evening interim, or "quiet," period* (beginning about 13 min after sunset and ending about 20 min later), which is characterized by the water column being essentially deserted of fishes; and 3) *the emergence of the nocturnal fishes* (from about 33 to 50 min after sunset), which begins when the surge of nocturnal fishes, mostly *Myripristis* spp., rise into the water column. In the morning, the sequence is reversed, being: 1) *the shelter-seeking of the nocturnal fishes* (from about 50 to 30 min before sunrise), which ends when the last of the nocturnal fishes in the water column, usually *Myripristis* spp., have descended to cover; 2) *the morning interim, or "quiet," period* (beginning about 33 min before sunrise and ending about 20 min later), when the water column is essentially deserted; and 3) *the emergence of the diurnal fishes* (from about 13 min before sunrise to a point soon after sunrise), which begins when the surge of diurnal fishes, mostly acanthurids, rise into the water column.

5. In the evening, diurnal fishes, both within and between species, seek cover in an order that corresponds roughly to increasing size. That is, the larger fishes seek cover last. In the morning, the same fishes emerge from cover in an order that corresponds roughly to decreasing size. That is, the larger fishes emerge from cover first.

6. There is some territorial aggression among diurnal fishes during evening twilight that expresses conflict over resting spots. However, the aggression is minimal considering how many fishes settle into resting positions on the reef at this time. Limited evidence suggests that overt conflict is reduced because at least some individuals have established resting spots.

7. Reef fishes are most vulnerable to predators during twilight because mechanisms that reduce predation during the day and night are less effective during the transition between these two major segments of the diel cycle. The interim, or "quiet," period in Kona is the time of greatest potential danger and corresponds in time relative to sunrise and sunset to the period when schooling fishes in the Gulf of California are under heaviest attack. Similar overt predator-prey interactions are relatively infrequent at this time in Kona because the schooling prey and the predators that exploit them are not major elements of the Kona fauna.

8. The well-ordered pattern of twilight activity among Kona reef fishes, which is essentially the same among tropical reef fishes in other seas, has been shaped by a historic threat from crepuscular predators. In areas where predators are only a relatively mild threat, as in Kona, twilight activity follows the same pattern as it does in areas where predators are a severe threat, as in the Gulf of California. Because predator-prey relations among fishes have responded throughout time to certain basic, unchanging phenomena, the similarity of twilight activity patterns among fishes on widely separated reefs today is the result of a long evolution that in any one area transcends the existing situation and species.

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CONSIDERATION OF THREE PROPOSED MODELS OF THE MIGRATION OF YOUNG SKIPJACK TUNA (*KATSUWONUS PELAMIS*) INTO THE EASTERN PACIFIC OCEAN[1]

F. WILLIAMS[2]

ABSTRACT

Previous evidence suggested that most exploited skipjack tuna (*Katsuwonus pelamis*) in in the eastern Pacific Ocean have a central Pacific spawning origin. Three models are now proposed of the migration of young skipjack into eastern Pacific fishery areas; these are (i) the active migration model, (ii) the passive migration model, and (iii) the gyral migration model. Data utilized and theories advanced in the detailed development of the models are discussed. Mechanisms and timing in all three migration models are dependent on oceanographic conditions and events in the central-east Pacific, which thus have a controlling effect on migration success of incoming young fish. Current skipjack research cruises, in part designed to test the validity of the models, are outlined.

Skipjack tuna (*Katsuwonus pelamis*) are widely distributed in tropical and subtropical surface waters of world oceans. In the Pacific Ocean there are three principal fisheries: the Japanese home islands fishery, including the Ryukyu-Tokara-Izu-Bonin Islands (1956-1969, range 87,000-252,000 short tons); the Hawaiian Islands fishery (1956-1969, range 3,000-8,000 short tons); and the eastern Pacific fishery from California to northern Chile (1956-1970, range 52,000-132,000 short tons). In addition, there are skipjack fisheries off Taiwan and the Philippines, developing ones of various sizes in Micronesia, Melanesia, and Indonesia, and subsistence fisheries in many other island groups, such as the Society-Tuamotu Islands. With the regulation of yellowfin catches in the eastern Pacific through an annual catch quota and the general decline in Japanese longline catch rates of tunas, the fishing industry has been showing increased interest in skipjack for a greater share of total tuna catches.

Fujino (1967, 1970, and in press) has shown that genetic studies indicate a subpopulation of skipjack in the western Pacific distinct from that present in the central-east Pacific. Seasonal mixing of the two subpopulations, or replacement one by the other, is considered to take place in the area immediately to the east of an arc through the New Hebrides-Solomon-Caroline-Mariana-Bonin Islands chains to the waters off the northeast coast of Japan.

The hypothesis on North Pacific skipjack advanced by Kawasaki (1965a, b) proposed a transpacific population with a common element and radiation outwards of juveniles from a central Pacific spawning area with eventual return to that area of sexually mature fish. This aspect of Kawasaki's hypothesis does not seem tenable, in view of Fujino's work. It is possible though that Pacific-wide changes in environmental conditions may cause apparently similar fluctuations in skipjack abundance in different areas through effects on recruitment and distribution.

Schaefer (1963) and Rothschild (1965) reported on the structure of skipjack populations in the central-east Pacific and stated that skipjack in the eastern Pacific fishery have a central Pacific origin. This inference was based primarily on the indicated general lack of spawning

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in the eastern Pacific (east of long 130°W), by few fish with fully developed gonads (Schaefer and Orange, 1956; Orange, 1961) and few larvae (Matsumoto, 1958; Klawe, 1963), and the occurrence of some long distance tag returns indicating movements from Baja California to the central Pacific, including the Hawaiian Islands (Schaefer, 1963; Inter-American Tropical Tuna Commission, 1964). (Subsequent data on skipjack larval distribution and tagging have supported the inference for a central Pacific origin.) Schaefer's and Rothschild's opinions differed, however, as to whether skipjack from south of the equator entered into this common genetic pool. Fujino (1970) indicated there was no genetic evidence to suggest South Pacific skipjack are not part of the central-east Pacific subpopulation(s) and also stated that present evidence for any differences between skipjack from varying parts of the central-east Pacific (Hawaiian Islands, Line Islands, Ecuador, Baja California) is very slight.

Rothschild (1965) generated a hypothesis on the movements of skipjack within the central-east Pacific (Figure 1). He postulated that skipjack juveniles in the central Pacific are continually dispersing from that region and that a large component of them move eastward into the eastern Pacific, where one contingent enters the Baja California fishery and the other the Central-South American fishery. Recruitment to these fisheries commences at about 35-40 cm (Rothschild, 1965; Joseph and Calkins, 1969). The fish remain in the eastern Pacific until they are maturing or mature at 40-65 cm, which probably is for 12 months or less, but only rarely longer than this. Thereafter, the fish leave the region and return to the presumed spawning grounds in the central Pacific and do not usually return to the eastern Pacific surface fishery.

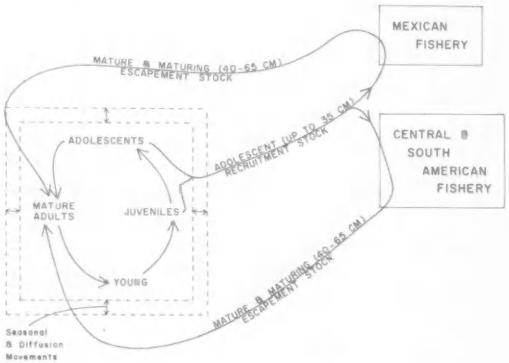

FIGURE 1.—Diagram showing the flow of skipjack between the central Pacific and the Mexican and South American fisheries of the eastern Pacific Ocean (from Rothschild, 1965, Figure 2).

The boundary between the two eastern Pacific fishery groups appears to be centered on the Gulf of Tehauntepec, with the northern fishery mainly off Baja California and the southern one mainly off Central America and Ecuador. There appears to be little mixing between these fishery groups as seen by lack of intergroup returns (Joseph and Calkins, 1969; Fink and Bayliff, 1970) and morphometric analysis (Hennemuth, 1959) even though genetic data (Barrett and Tsuyuki, 1967; Fujino, 1970) show no gross intergroup differences. The degree of geographic separation of the groups varies considerably from year to year (Williams, 1970).

According to Rothschild (1965) the mechanism causing the split into northern and southern fishery groups could be many and not fixed in time or space. The extent to which they split the skipjack into the northern and southern groups could be a function of the north-south and temporal distribution of the incoming eastward-moving recruits. One possible splitting mechanism was considered to be the warmwater cell (surface temperatures $>28°C$) in the vicinity of lat 15°N off the Central American coast (see monthly average temperature conditions, Wyrtki, 1964). Blackburn (1962) suggested that this same warmwater cell impeded north-south movement and intermingling of the groups, the extent of which varied with surface temperature from year to year. Williams (1970) has shown that in the eastern Pacific, skipjack occur at all temperatures $>17°C$ with the majority from 20° to 30°C, though apparent abundance was only high up to 29°C. This increase of 1°C, from 28° to 29°C, in the limiting temperature for skipjack in quantity is important. The monthly average temperature charts of Wyrtki

(1964) show the area of water >29°C is much less extensive than that >28°C, particularly offshore to the westward, and also in duration, e.g., in April-May 28°C water normally extends out to long 118°-119°W, but 29°C water only to long 102°-103°W. Even if the 28°C water was accepted as a splitting mechanism, it is shown in a subsequent section that not being fully developed in offshore extent (to long 120°W) until April, it is too late to initiate the separation of incoming recruits into the northern and southern fishery groups.

ENTRY OF RECRUITS INTO AREAS OF FISHERY

Fink and Bayliff (1970) discussed the migration of skipjack in the inshore areas of the eastern Pacific based on tagging experiments from 1952 to 1964 (Figure 2). The data are substantial for the immediate coastal areas of the fishery but much less so for the offshore island areas. In the northern fishery (Figure 2A) the principal entry point for small fish is the Revillagigedo Islands (lat 19°N, long 111°W) in April, and from there they move inshore from about May to June. In the southern fishery (Figure 2B) the situation is more complicated, but the entry of small fish only appears confirmed for the northern Panama Bight in April (and also into the Gulf of Guayaquil).

In view of the indications of size-specific movements through certain areas of the eastern Pacific fishery (Rothschild, 1965), the skipjack length-frequency data of the Inter-American Tuna Commission (IATTC) for 1954-1967 were reexamined, albeit subjectively, to obtain possible information on time of entry of young fish. Size range in the eastern Pacific fishery is about 36-74 cm, but more usually 42-62 cm. [Eastern Pacific length data from the U.S. fleet are selective because of the California minimum

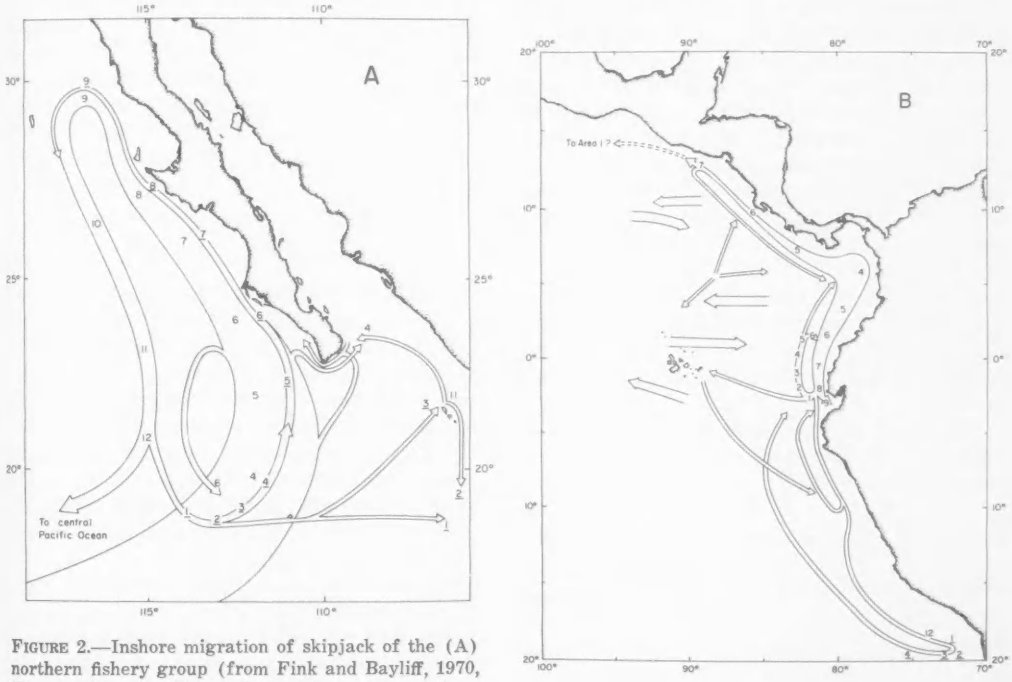

FIGURE 2.—Inshore migration of skipjack of the (A) northern fishery group (from Fink and Bayliff, 1970, Figure 89) and (B) southern fishery group (from Fink and Bayliff, 1970, Figure 90) based on tagging data; numbers refer to months.

landing size of 4½ lb (≈45-50 cm), but in South American landings by local boats (Manta) the smallest fish are about 36 cm.]

The length-frequency data in general show that the smallest skipjack in the northern fishery are found offshore at the Revillagigedo Islands from March to June. The modal size of these fish is <50 cm, and often between 40 and 45 cm. From March to May some similar sized fish are also seen in catches from adjacent inshore areas between the southern Gulf of California and Cape Corrientes (lat 25° to 20°N). Most of these small fish subsequently migrate into the skipjack fishery off western Baja California. In October (± 1 month) of most years there appears to be a small entry of fish, modal length ≤45 cm, at the Revillagigedo Islands, which is often reflected in the length-frequency distributions for November in the Baja California area.

In the offshore areas of the southern fishery a main influx of small fish, modal lengths <50 cm, appears to be at the Galapagos Islands from November to April with the peak in January and February. Data from the adjacent inshore area off Ecuador subsequently seems to reflect this entry of small fish. In addition, small numbers of skipjack of modal lengths ≤45 cm often occur in August (± 1 month) off Ecuador, as well as in Peru-northern Chile catches in abnormally warm oceanographic years. In the Cocos Island area fish of modal lengths ≤45 cm are found in January and February (there is some evidence this entry of small fish starts in November or December and lasts into March). Fish in this same size range subsequently occur in some years in the Gulf of Panama from April to June.

The apparent times and places of entry of small skipjack into the eastern Pacific fisheries are summarized below:

Fishery	*Area of entry*	*Time of entry*
Northern	Revillagigedo Is.	March-June October (± 1 month)
Southern	Ecuador	August (± 1 month)
	? Galapagos Is.	
	Galapagos Is.	November-April (peak January-February)
	Cocos Is.	November-March (peak January-February)

These findings are generally consistent with those of Fink and Bayliff (1970) for the northern fishery and expand those for the southern fishery.

Work on the growth of central-east Pacific skipjack using length-frequencies has been complicated by the problem of size-specific movements through the fisheries. Additionally, there is as yet no secondary age estimation method for the species. Recent work by Yoshida (1971), on young skipjack from the stomachs of long-line-caught billfish in the central Pacific, has indicated that a 1-year-old skipjack may be about 31 cm. This is a similar length to that deduced from tagging data (averaged) for eastern Pacific fish by Joseph and Calkins (1969), who discuss the various deduced growth rates for the species, whereas Rothschild (1967), on the basis of short-term tag returns, indicated about 44 cm for a 1-year-old fish. Depending on the accepted growth rates, recruits to the eastern Pacific fisheries might thus be between 8 and 15 or 12 and 24 months old on entry and between 15 and 24 or 24 and 36 months old when departing the region for first spawning in the central Pacific.

CIRCULATION IN THE EASTERN TROPICAL PACIFIC

The oceanography of the eastern equatorial Pacific was reviewed by Wyrtki (1966, 1967). The circulation of intertropical surface waters shows the west-flowing North and South Equatorial Currents (NEC, SEC) with between them the relatively narrow (180-360 miles) east-flowing North Equatorial Countercurrent (NECC) at about lat 5°-10°N (Figure 3). At or just south of the equator below a depth of 20-50 m is the Equatorial Undercurrent (EUC) (Cromwell Current) with eastward flow.

However, Wyrtki (1965, 1966) indicated marked seasonal fluctuations in surface currents in the eastern Pacific. From June to December the NECC is fully developed through to the central American coast, while during January and May it is intermittent, and from February to

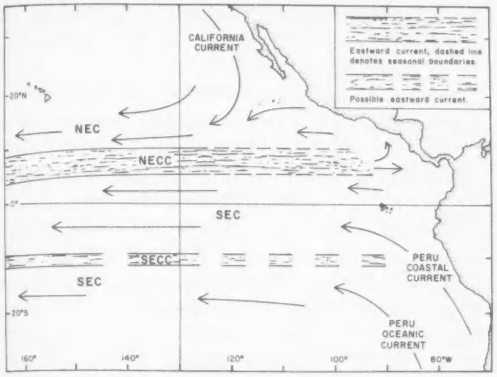

FIGURE 3.—Schematic chart of surface circulation in the tropical central-east Pacific Ocean. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent.

April absent, east of long 120°W. Although Tsuchiya (1968) showed that below a depth of 50-100 m the NECC eastward transport is continuous throughout the year, more recent calculations of geostrophic flow from EASTROPAC data (M. Tsuchiya, unpublished data and personal communication) show that the subsurface transport is separate (deeper and slightly farther south) and that the surface NECC does cease or become minute and variable from January to May.

A striking relationship between development of the surface NECC and the latitudinal position of the Intertropical Convergence Zone (ITCZ) (meteorological equator) at the meridian of 120°W was presented in Wyrtki (1965). The NECC ceases east of long 120°W with the annual movement of the ITCZ south of lat 8°N about January, and when it returns north of lat 8°N about May, the NECC is reestablished. Hence, variations in the ITCZ position at long 120°W may be reflected in the time of cessation and resumption of the surface NECC, i.e., duration of the interruption. Abrupt interruption of the current is apparently not the case, and at least in January and May, it is weak and intermittent, and eddies and meanders may occur. [Superimposed on the overall monthly trend is also variability due to short-term (daily) fluctuations in ITCZ position.] Monthly ITCZ positions at long 120°W and NECC position based on Wyrtki (1965, Figure 18) are reproduced here as Figure 4, together with ITCZ monthly positions based on a 77-year mean of observations from the National Weather Records Center and prepared by the Goddard Space Flight Center, NASA (Allison et al., 1969). The position of the ITCZ is controlled by the variations in the location and strength of the wind fields in the central-east Pacific, the northeast and southeast trades, and the pressure fields associated with them.

Wyrtki (1966) stated the California Current is strong and penetrates farthest south and contributes most of the water to the NEC in the period February to April. The California Current is weak and located north of lat 20°N from August to December while in January and May-July it shows intermediate positions and strengths.

Tsuchiya (1968, 1970) has reviewed the present scanty information on the zonally narrow

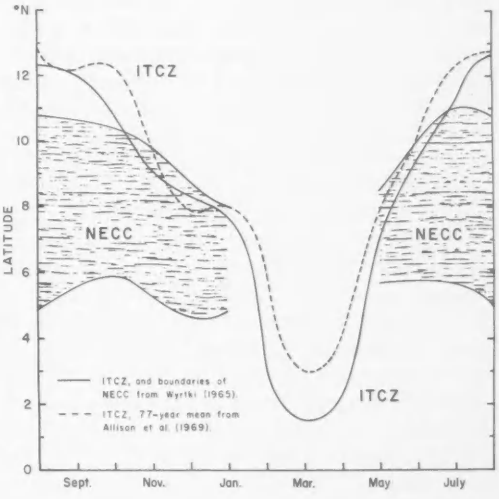

FIGURE 4.—Seasonal variations in the position of the Intertropical Convergence Zone (ITCZ) and of the boundaries of the North Equatorial Countercurrent (NECC) at long 120°W.

(2°-3° of latitude) South Equatorial Countercurrent (SECC), and shows that there appears to be a subsurface component at about lat 5°S. The surface SECC is ill-defined in the eastern Pacific (east of long 140°W) and M. Tsuchiya (personal communication) states that so far there is no physical oceanographic evidence from EASTROPAC data to confirm its existence.

FACTORS INFLUENCING SKIPJACK DISTRIBUTION

Blackburn (1965) considered that simple oceanic properties, such as temperature, directly determine overall limits of distribution of tunas, but that oceanic features and processes, among them surface currents, determine temporal and spatial differences in abundance within these limits. Though tuna distributions sometimes follow currents, he thought such relationships were often indirect, i.e., through property distributions associated with the currents. Blackburn was also of the opinion that the case for causal relationship between distribution of water masses and that of tuna species was inconclusive. However, Nakamura (1969) hypothesized that (i) tunas, according to species and life history stage, have their centers of distribution in distinct current systems or water masses, which provide specific habitats for them, and (ii) migrations of tunas are of two types, within a habitat and between habitats.

The consideration is now of the oceanographic factors influencing possible routes taken by skipjack when migrating from the central to the eastern Pacific. Throughout the tropical central-east Pacific near-surface temperatures are optimal for skipjack, except along the equator west of the Galapagos Islands out to long 100°W in certain months, and, of course, in the cold waters of the Peru Current. Given optimal temperatures, then the next factor governing distribution is probably the supply and distribution of food (Blackburn, 1965, 1969a, b). Adult skipjack are carnivorous on macrozooplankton and micronekton, and there is no reason to believe this does not hold for juvenile and adolescent skipjack, although the size range of the diet is probably smaller, that is more zooplankton. Even in adult fish Yuen (1959) for the Hawaiian Islands, Alverson (1963) for the eastern tropical Pacific, and Nakamura (1965) for the Marquesas and Tuamotu Islands presented evidence of smaller proportions of crustaceans and/or molluscs in large skipjack (over 60 cm) than in small ones. Contradictory evidence is found in the results of Waldron and King (1963), which showed no significant differences in the principal components of stomach contents of central Pacific skipjack.

Previous work in the equatorial central Pacific (Sette, 1955, 1956, and references therein; King and Hida, 1957; King, 1958; King and Iversen, 1962; Murphy and Shomura, 1972) indicates that there occur zonal "productivity" bands, representing various stages from nutrient enrichment to trophic levels, such as those represented by zooplankton and micronekton, which may be correlated with fish distribution. The principal such band normally exists between the southern edge of the NECC and a few degrees either side of the equator. Within this range there are latitudinal displacements of the "productivity" band (and its components) with time, probably as a function of the occurrence of the prevailing wind systems, the southeast and northeast trades (see Murphy and Shomura, 1972, for detailed discussion). A second, less intense[3] and more transient (or poorly documented) "productivity" band appears to exist close to the pycnocline at the NECC/NEC boundary. Its intermittent nature may be due to the nature of the mixing processes, such as ridging (Cromwell, 1958). Reid (1962) presented charts of average zooplankton volume (for upper 150 m) that indicated the existence of these two zonal bands in the central-east Pacific. In addition, he indicated a narrow zonal "productivity" band from lat 15°S in the east to about lat 10°S in the central Pacific. Close to the shore the zonal bands merged with features related to coastal distribution.

EASTROPAC zooplankton and micronekton data published in Atlas form (Love, 1970, and in preparation) in general confirm the existence of the northern and equatorial zonal "productiv-

[3] May be due to biased sampling procedures (Blackburn and Laurs, 1972; Maurice Blackburn, personal communication).

ity" bands in the eastern tropical Pacific. More detailed statistical treatment (for significance of interactions) of EASTROPAC primary productivity, phytoplankton, zooplankton, and micronekton data (Owen and Zeitzschel, 1970; Blackburn et al., 1970) from the western EASTROPAC area (lat 16°N-3°20'S, long 100°30'-121°30'W) show clearly the equatorial zonal band(s). However, the band at the NECC/NEC boundary is not clear at trophic levels other than zooplankton, and possible reasons for such anomalies are discussed in some detail. In addition, Owen and Zeitzschel (1970) pointed out that latitudinal effects may have been eliminated due to selection of geographic zones which do not coincide with natural (zonal) current systems.

Blackburn and Laurs (1972) have discussed the distribution of that part of the EASTROPAC micronekton catches which can be classified as skipjack forage. They not only confirm the existence of equatorial bands of high forage concentrations just north of the equator, and occasionally south of it, but also of a band at the NECC/NEC boundary, particularly in daytime catches.

There is some biological evidence from EASTROPAC data of increased "productivity"-zooplankton, micronekton, occurrence of birds (Love, 1970, and in preparation; R. M. Laurs, personal communication)—at certain times between lat 5° and 15°S, particularly lat 12°-14°S, the general region where the surface SECC might be expected. Such increased "productivity" could occur if a divergence existed in these latitudes, say at the southern SECC/SEC boundary.

Generally in the EASTROPAC area standing stocks decreased from east to west (Blackburn et al., 1970), that is from inshore to offshore, as did zooplankton in the charts of Reid (1962).

PROPOSED MIGRATION MODELS

ACTIVE MIGRATION MODEL (Figure 5)

Skipjack larvae are rare east of long 130°W (Matsumoto, 1966; Ueyanagi, 1969), and this generally appears to be borne out by the results of the EASTROPAC expedition (Love, 1970, 1971, and in preparation). It would seem, therefore, that adult skipjack spawn in the surface waters to the west of long 130°W, which in some way must be ecologically suitable for optimum survival and development of the larvae. In this model it is assumed that these larvae, and early juveniles, are maintained within the central Pacific by some passive migration system, perhaps related to the equatorial zonal current systems, eddies associated with island wakes, as well as diel vertical migrations.

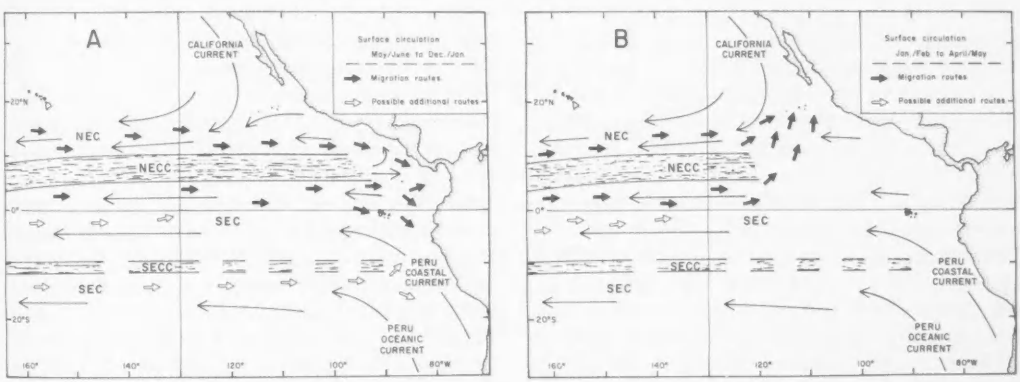

FIGURE 5.—Active migration model: (A) routes of young skipjack into the southern fishery and (B) routes of young skipjack into the northern fishery. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent.

At a certain size a large component of these juveniles start an active migration eastwards which ends with them on the feeding grounds of the northern and southern fisheries off the American continent. The size at which this active migration commences is not known, but with recruitment to the fisheries at 35-40 cm it is probably at <30 cm.

When in the eastern Pacific skipjack are feeding heavily, and this appears related to both the food requirements of the adolescent fish for normal growth and for the early development of the gonads. The departure of the fish with maturing gonads from the feeding grounds is attributed to a reproductive drive to return to the central Pacific where final maturation of the gonads and spawning must take place.

Richard S. Shomura and Richard A. Barkley (personal communications), with arguments based on central Pacific data, have suggested two spawning groups (northern and southern) are present in the central-east Pacific skipjack subpopulation(s) with considerable geographic overlap in equatorial areas. One group spawns during the northern summer, peak in July, and the other in the southern summer, peak in January. There is some slight evidence (Orange, 1961) that skipjack in the eastern Pacific fisheries are from two such spawning groups. Fujino (in press) has indicated that in the western Pacific subpopulation of skipjack there are two spawning groups (northern and southern) with a large overlap in geographic distribution.

Even though larval and early juvenile skipjack obviously make diel vertical migrations (Wade, 1951; Matsumoto, 1958; Strasburg, 1960; Ueyanagi, 1969, 1970; Higgins, 1970), the lower end of the temperature range is thought to be restricted to about 24°C, at least for larvae (Ueyanagi, 1969; Richards, 1969; Eric Forsbergh, personal communication). However, the adolescents arriving on the feeding grounds of the eastern Pacific fishery seem to have attained a physiological condition which permits them to exist at ambient temperatures down to 20°C, and occasionally 17°C, which are found in the near-surface waters of these zones (in other areas of the world, such as Tasmania, they may be as low as 15°C, Robins, 1952). Ability of skipjack to tolerate low ambient temperature (conserve internal heat) is probably a function of size (sequential physiological events), and this is also important in relation to the depth capability of the fish in its search for food at various life history stages. It is worth noting that skipjack have been shown (see below) to maintain body muscle temperatures considerably above ambient water temperatures:

Skipjack length (cm)	*Ambient water temperature (°C)*	*Body muscle temperature (°C) above ambient*	*Source*
43-47	25.6	8.5-9.1	Stevens and Fry (1971)
47-56	19.4-30.6	5-6	Barrett and Hester (1964)
71-76	26.6	4-8	Stevens and Fry (1971)
--	18.5, 29, 30	11.7, 7.8, 8.3	Carey et al. (1971)

Obviously the principal factors to be explained eventually in the the active migration model are those which induce the juvenile skipjack to migrate out of the central Pacific. Such a genetically fixed behavioral pattern undoubtedly would be a response to a summation of effects caused by exogenous and endogenous stimuli. Baggerman (1960) considered that migration, basically a function of locomotion and orientation, only occurs when fish are in the proper physiological condition and subject to external "releasing" factors (stimuli). This physiological condition, in turn, is brought about by endocrinal activity initiated by endogenous rhythms and external "priming" factors. This concept of causation of migration possibly may well apply in the case of tuna.

Hoar (1959) noted that for fishes with mass cyclical migrations at certain life history stages (such as reproduction, movement from nursery to feeding grounds) changes in endocrine secretions (gonadal, thyroidal) appear to play a major part in the generalized appetive behavior associated with migration. Woodhead (1959a, b) discussed the role of the thyroid in the migrations of mature and immature Barents Sea cod described by Trout (1957). It appeared that the "dummy run" contranatant migration of the im-

mature cod was under thyroid control, a distinct cycle in thyroid follicular cell height being observed although less than in mature fish. Woodhead (1959a) and Woodhead and Woodhead (1965) suggested production of such an active migration could be due to a general increase in swimming activity and in reaction to water currents (particularly a tendency to swim against them) caused by the increase in thyroid hormones. The thyroid in tuna, unlike most teleosts (including the cod), is a discrete bilobed structure (Honma, 1956—bluefin tuna; Williams, unpublished—skipjack and yellowfin tuna). If, as the juvenile skipjack approaches the size associated with first migration, the thyroid becomes more active and one effect of this is to initiate a similar behavioral response as in the cod (increased locomotor activity), then there would be a subsequent demand for more food if the growth of the animal is to be continued. At such time it is suggested that the increased food requirements—amount, type, size—cannot be supplied in the central Pacific near-surface waters, or that the young skipjack come increasingly into competition for the available food with other species and also their own adults. (See also discussion of evolution of migration patterns in Rothschild and Yong, 1970.) Additionally, the endocrine induced internal stimuli may also act to lower thresholds for recognition of changes in environmental conditions to the magnitude of those found in the equatorial central Pacific.

Sequences of events, such as mentioned above, could possibly trigger the active migration of juvenile skipjack out of the central Pacific—the main component being to the feeding grounds in the neritic eastern Pacific. It is proposed that the migrating skipjack juveniles are principally located in the equatorial areas of the west-flowing NEC and SEC. With near-surface temperatures optimal, except at the equator west of the Galapagos Islands at times of intense upwelling, the fish are located within or close to the equatorial and northern "productivity" bands described previously. In view of the apparent intermittent nature of the northern band, it is possible that the incidence of small, but frequent fronts may also act as concentrating mechanisms for food organisms normally observed at a low density in this area, lat 5°-10°N (Murphy and Shomura, 1972). Skipjack may also be associated with the possible "productivity" band around lat 10°-15°S.

The mechanisms which maintain the overall eastward orientation of the skipjack in an offshore oceanic area (in the absence of reference points) are unknown, although as Hoar (1953) commented "fish possess an elaborate and delicate array of highly specialized peripheral sense organs and appendages" and these could all be involved in some type of navigating ability in tuna. In this respect the probable role of the pineal apparatus of tunas as a photoreceptor (Rivas, 1953) should not be overlooked. Royce, Smith, and Hartt (1968) in a discussion of possible guidance mechanisms in oceanic migration models of Pacific salmon concluded that they may depend on electromagnetic cues from ocean currents and that responses to all migratory cues are inherited. Recent work by Yuen (1970) on tracking of small skipjack (with ultrasonic tags and continuous-transmission frequency-modulated sonar) moving on and off banks in the Hawaiian Islands lead him to imply that skipjack can navigate and have a sense of time.

It is hypothesized that incoming juvenile skipjack move continuously eastwards past the meridian of long 130°W, orientating largely to the zonal "productivity" bands (northern and equatorial) until entering the offshore areas of the southern fishery from August to April. However, the interruption or cessation of the surface NECC east of long 120°W in the period January-February to April-May might be expected to disrupt the orientation and movement of incoming skipjack juveniles, mainly through significant changes in the position or continuity of the "productivity" bands and food-concentrating mechanisms. It is at this period of the year that recruitment to the northern fishery is postulated.

Certainly the cessation of the NECC would cause the deepening of the mixed layer in the vicinity of the previous northern boundary of the NECC, and hence the elimination of possible ridging and subsequent increased biological productivity, though it is very difficult to estimate the lag period. In the case of the equatorial band (east of long 120°W) the annual southward

passage of the ITCZ causes a rapid change from predominantly southeast trades to either northeast trades or light easterly winds/doldrumlike conditions. In the former case, there would be divergence at the equator and formation of a weak convergence some distance south of the equator, while in the latter case there would be equatorial divergence but no convergences. Either way it would seem that there might be significant disruption of the "productivity" bands. However, EASTROPAC data do not show this very clearly, perhaps due to the lag period in the establishment of the higher trophic levels.

If a surface SECC is present in the eastern Pacific (even seasonally) then eastward movement of juvenile skipjack could possibly take place in the SEC near a southern "productivity" band (at the SECC/SEC southern boundary). Subsequently there would be an active migration of juveniles from near the SECC terminus into the southern fishery. However, water temperatures alone could prevent any direct recruitment from this area to the southern fishery during part of the southern winter. [In this and subsequent migration models speculations are not made on skipjack distribution south of the possible SECC/SEC southern boundary.]

Tuna have to swim continually to ensure ventilation across the gills and to maintain hydrostatic equilibrium, and maximum speeds in excess of 10 body lengths per second (bl/sec) have been reported (Blaxter, 1969, and references therein). For the closely related little tuna (*Euthynnus affinis*), Magnuson (1970) reported the minimum speed for hydrostatic equilibrium in a 42-cm fish was about 1.4 bl/sec and calculated for a 10-cm fish it would be about 3 bl/sec. After feeding, the average speed of the same captive fish increased to about 2 bl/sec, while Walters (1966) recorded for a 40-cm fish a speed of 5.9 bl/sec on a feeding run on dead fish and a maximum speed of 12.5 bl/sec. Magnuson (1970) also pointed out that the little tuna appears to spend most of its time swimming at speeds near the minimum hydrostatic speed and relatively little near the maximum. For captive skipjack of 38, 39, and 48 cm, John J. Magnuson (personal communication to Maurice Blackburn) indicated that the observed mean speed was about 2 bl/sec; for calculations for model fish the minimum speed for a 15-cm juvenile skipjack would be about 3 bl/sec. Actively migrating juvenile skipjack may be expected to have a narrow range of theoretical minimum speed, from 2 to 3 bl/sec.

The tracking of 40-42 cm skipjack in the Hawaiian Islands by Yuen (1970) showed that movement off a bank at night, principally from 1800 to 0200 hr, was mainly near the surface and without frequent directional changes, at speeds equivalent to about 1.5-6.0 bl/sec. However, during daylight, apparent speeds fell well below Magnuson's calculated minima which, Yuen concluded, must indicate considerable turning from a straight line track, presumably due to food searching and feeding—[skipjack are primarily daylight feeders (Nakamura, 1962)]. In addition, there was a greater variability in depth during the day than the night. On a recent cruise (Williams, 1971) small groups of skipjack were observed from the deck and underwater bow chamber swimming just ahead of the RV *David Starr Jordan* for considerable lengths of time. For the size of fish involved, a sample of four ranged from 60 to 64 cm FL, and the ship's trolling speed of 6½ knots, the skipjack were maintaining speeds of about 5.5 bl/sec.

In view of the above data it is considered reasonable to assume a mean swimming speed for incoming young skipjack equivalent to about 3 bl/sec "made good" in the direction of the oriented movement (migration) over the 24-hr period, i.e., about 50 miles per day. Hence, the first recruits entering the offshore areas of the southern fishery at the beginning of August may well have passed the meridian of 120°W about 6 weeks earlier, i.e., in mid-June shortly after the surface NECC is reestablished east of that meridian. Similarly, the last recruits to this fishery, in entering the offshore areas about the beginning of April, would have passed long 120°W about mid-February close to the time of, or shortly after, the interruption of the surface NECC east of that point. Thus, at the time of entry of the principal component of recruits from November to April, peak January and February, the surface NECC is established

east of long 120°W. It is considered that from February to April-May, when the surface NECC is absent east of long 120°W, the juvenile skipjack are being recruited to the northern fishery where they occur in the offshore area (the Revillagigedo Islands) from about March to May-June (arrival April-June onwards in Baja California). From long 120°W (lat 0°-10°N) about 2-4 weeks would be required for the skipjack to reach the Revillagigedo Islands, which agrees closely with the actual occurrence of juvenile skipjack at that location.

It will be recalled that one of the possible splitting mechanisms proposed by Rothschild (1965) was the >28°C surface water cell off Central America, but which it has been shown is not well developed out to long 120°W until April. Thus, even if >28°C water was limiting for skipjack (in quantity), and not >29°C water as shown recently (Williams, 1970), then that cell could not initiate the split as early as February.

The occurrence of small size fish at the Revillagigedo Islands in October (± 1 month) in some years is not accounted for in this model. This could occur if in midsummer some recruits destined for the southern fishery and located close to the northern boundary of the NECC (about lat 10°N) were deflected northward from their migration route by the >29°C water cell normally stretching southward from Central America at that time.

It is proposed that a gating or shunting mechanism operates at about long 120°W across the equatorial and northern migration routes of juvenile skipjack. When the NECC is continuous east of long 120°W, the gate is open and recruitment is to the southern fishery (Figure 5A). Then, with the annual southward movement of the ITCZ, the surface NECC ceases east of long 120°W, and the gate is closed from about February to April-May. Recruitment to the southern fishery ceases and instead the flow of recruits is to the northeast and into the northern fishery (Figure 5B). When the gate is closed there is a loss of west-east orientation due to changes consequent on the breakdown of the surface NECC, such as the loss of the current boundary conditions (with NEC and SEC), possible interruption (total and partial) of the zonal "productivity" bands, loss of food concentrating mechanisms (minor fronts), etc. The principal question then is how the recruit skipjack become oriented to the northeast, i.e., towards the Revillagigedo Islands. There could well be random dispersal of incoming recruits when the gate closes at long 120°W, with only a small proportion moving northeastwards into the California Current Extension and the majority eventually recycling to the central Pacific. Possibly those fish moving northeast pick up a "food bridge" linking the area around long 120°W in the vicinity of the NECC with the Revillagigedo Islands and Baja California. Such a "food bridge" could be provided offshore by the pelagic stages of the red crab (*Pleuroncodes planipes*) which are found in the California Current Extension (Longhurst, 1967, 1968; Longhurst and Seibert, 1971), the gradient of abundance of which increases towards the northeast (shorewards). It will be remembered that the California Current Extension is strongest and farthest to the southwest at this period. Red crab are known to form a large part of the diet of skipjack in Baja California waters during the fishing season (Alverson, 1963). A "food bridge" facilitating the northeast movement of recruit skipjack, because of survival value, may have become an inherited behavioral response when west-east orientation is lost around long 120°W in the period February to April-May.

One possible objection to the gating mechanism could concern efforts by the juvenile skipjack to dive below its effects. This is considered unlikely in view of adverse temperatures (<20°C) at depths where subsurface eastward flow is continuous and low oxygen concentrations at relatively shallow depths, at least as far south as lat 10°N. Oxygen content as low as 3 ml/liter has been suggested as possibly limiting for skipjack (Commercial Fisheries Review, 1965).

PASSIVE MIGRATION MODEL (Figure 6)

In this model it is hypothesized that larval and juvenile skipjack are passively carried eastward in the equatorial countercurrent(s) from the central Pacific spawning grounds to the offshore areas of the eastern Pacific fisheries.

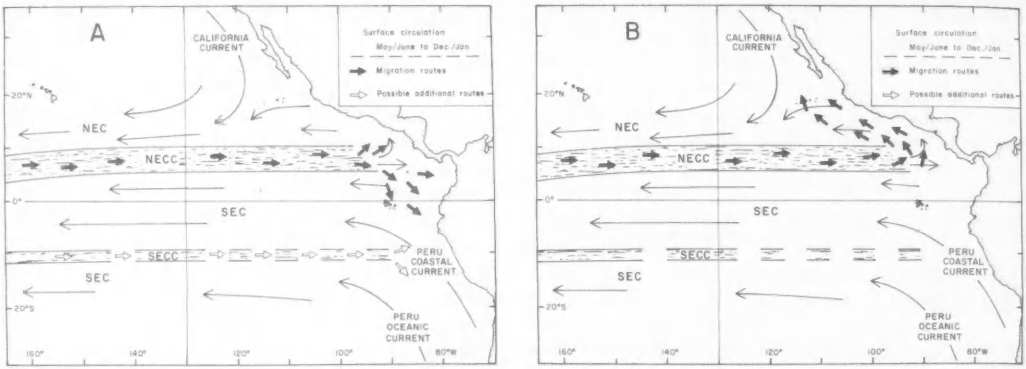

FIGURE 6.—Passive migration model: (A) routes of young skipjack into the southern fishery and (B) routes of young skipjack into the northern fishery. NEC = North Equatorial Current; NECC = North Equatorial Current; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent.

Many of the larval and early juvenile skipjack in the central Pacific would originate in, or be involuntarily transported into, the NECC and while developing in this current (few larvae are found east of long 130°W) would be transported eastward with it. Although generally increasing in a west-east direction the productivity, in terms of zooplankton, of the NECC appears relatively low (Reid, 1962), though the incidence of small fronts in the NECC area (Murphy and Shomura, 1972) would be likely locations for aggregations of food organisms. The rapidly growing and increasingly active skipjack juveniles would need therefore to forage extensively for food and, in view of the large numbers involved, this may also necessitate foraging near the edges of the "productivity" bands at or close to the NECC boundaries (the net transport of the fish would necessarily be eastwards).

The concept of a passive migration eastwards with the NECC eliminates the otherwise difficult question of orientation in the young fish. The dispersion of juveniles from the NECC, at its nearshore terminus, to the southern fishery would be relatively simple and similar to that in the active migration model (Figure 6A). For recruitment to the northern fishery the problem is more complex, depending on whether the fish destined for that area are transported when the NECC flows through to the coast or when it is intermittent or stopped east of long 120°W.

The surface current system along the central American coast (Wyrtki, 1965), at least from May-June to December, is such that juveniles could be passively transported from the nearshore terminus of the NECC to the Revillagigedo Islands area (Figure 6B). However, from about April to September warmwater cells (>29°C) of varying sizes off Central America would prevent transport of the juveniles close to the coast and with increasing offshore distance the risk would increase of passive transport westwards into the NEC and not to the Revillagigedo Islands. With the principal influx of fish into the offshore areas of the northern fishery being from March to June, approach to these areas would need to be taking place in the first months of the year, and this is in fact the time when the coastal current system appears least likely to support such a passive migration. Thus, there are some real problems of timing with the passive migration of young skipjack into the northern fishery in the NECC and Central American coastal currents.

If recruitment to the northern fishery takes place after the cessation of the NECC east of long 120°W, then it would require an active migration from the terminus of the NECC to the

Revillagigedo Islands (as proposed in the active migration model at this time of year). In the period prior to cessation, when the NECC is intermittent, juvenile fish would increasingly lose their eastward orientation, some being deflected into the weak NEC and with a sufficient northward component in the current might passively reach the Revillagigedo Islands, though such conditions would be short-lived.

Should recruitment to the northern fishery not take place at the time of cessation of the NECC, juvenile skipjack at that time being recycled to the central Pacific in the NEC and SEC, then all recruits to the eastern Pacific fisheries would have to be carried to the coast in the NECC in the period May-June to December-January. From long 130°W (eastern limit of spawning area) to 85°W (approximate NECC nearshore terminus) is 2,700 nautical miles and with an average NECC speed of ¾ knot, continuous passive movement over this distance would take about 5 months. This would make the arrival time at long 85°W October-November to May-June. Obviously transport time could be much longer than this, if, for instance, (i) daylight hours were entirely spent foraging and with near-zero movement eastward, and/or (ii) real transport rates were lower due to the effects of diel vertical migrations. From the NECC terminus at about long 85°W recruitment, even passive, to the initial southern fishery areas would probably take no more than 4-6 weeks, i.e., arrival November-January to June-August. But a passive drift from the NECC terminus northwest to the Revillagigedo Islands with surface currents about ½ knot would take in the order of 4-5 months, i.e., arrival February-May to September-December. However, the recruitment size of the skipjack to both northern and southern fisheries appears similar. Several factors might be proposed to account for this fact: (i) the spawning grounds of the fish found in the southern fishery are farther west in the central Pacific than those of the northern fishery, (ii) the early life history stages enter the NECC at different sizes, (iii) behavioral patterns of the juveniles (from the two groups) in the NECC are different, or (iv) the juveniles stay longer in the offshore areas of the southern fishery than the northern one. Of these proposals the first seems most likely, and would be understandable if the two fishery groups did represent parts of two spawning groups (northern and southern) as suggested earlier (see page 748). One feature which could influence the eastern boundary of the groups spawning in the central Pacific, particularly the southern one, would be the westward extent of the influence of low near-surface temperatures at and south of the equator due to equatorial upwelling and effects of Peru Current water.

A wide degree of geographic overlap of the spawning groups in the central Pacific would alleviate problems of recruitment of young stages of southern spawners into the NECC, as trans-equatorial migration might not then be involved to any extent. In addition, the occurrence of a surface SECC would provide a possible mechanism by which young stages of southern spawners from south of the equator could be carried passively into the eastern Pacific. However, as previously stated, the existence of a surface SECC has not yet been confirmed in the eastern Pacific.

Thus, as our knowledge stands at the moment the NECC could be passively carrying juveniles of both spawning groups into the eastern Pacific fisheries but at different sizes.

GYRAL MIGRATION MODEL (Figure 7)

The two models described so far are based on the assumption that larval or juvenile fish migrate, passively or actively, out of the central Pacific to feed in coastal surface waters of the eastern Pacific and then subsequently return to the central Pacific for first spawning. Between spawnings the adult fish diffuse outwards from the central Pacific to feed but rarely reenter the adolescent feeding grounds.

Incidental longline catches of skipjack through 1967 (Miyake, 1968; Walter M. Matsumoto, personal communication) indicate the widespread distribution of the adults. According to Matsumoto there is some evidence that areas of high longline catch-per-unit-effort of skipjack in the central-east Pacific show seasonal shifts which tend to coincide with the direction of flow of the

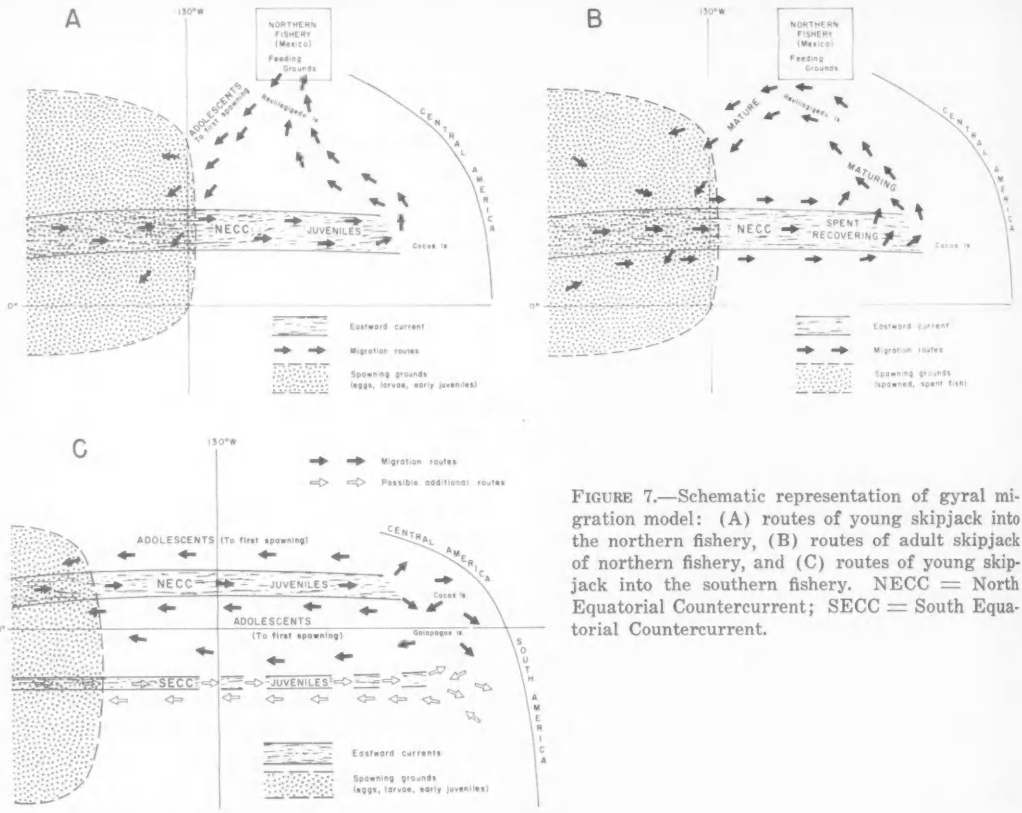

FIGURE 7.—Schematic representation of gyral migration model: (A) routes of young skipjack into the northern fishery, (B) routes of adult skipjack of northern fishery, and (C) routes of young skipjack into the southern fishery. NECC = North Equatorial Countercurrent; SECC = South Equatorial Countercurrent.

major ocean currents. Such movements appear to be counterclockwise in the southern hemisphere and clockwise in the northern hemisphere. The exception is in the eastern North Pacific where movement seems to be counterclockwise and corresponds to the narrow gyre of the northern equatorial water mass.

The above findings have suggested consideration of another type of model for skipjack, the gyral migration model, which involves all life history stages and both passive and active migrations. [Generalized gyral migration patterns are briefly discussed in Harden Jones (1968).]

For the northern fishery group it is proposed that the fish are moving counterclockwise around a zonally narrow equatorial gyre consisting of the NECC and the NEC, with the western limit some considerable distance west of long 130°W (possibly as far as long 170°W). In this model it is considered that mature skipjack spawn primarily in the northern spring-summer (May to October) in equatorial waters west of long 130°W, a large proportion of the subsequent larvae and early juveniles entering the NECC and with development then taking place in that current as proposed in the passive migration model (Figure 7A). The majority of the juveniles on reaching the terminus of the NECC are carried northwestwards with the coastal current off Central America, outside the warm-water cells >29°C. Movements of the adults would generally parallel the young stages, but they are in no way restricted to the NECC and may be found in a wide band covering the NECC

and adjacent areas of the NEC and the section of the SEC north of the equator (Figure 7B). This implies a navigational system in the adults. Thus, spent and spent-recovering fish would be expected in the areas immediately to the east of the spawning grounds. When the juveniles are off Central America and Mexico, the adults have also turned north and are located farther offshore and/or in deeper water. [It should be recalled that tag returns show little interchange of fish of the size caught in the eastern Pacific between the northern and southern fisheries (Fink and Bayliff, 1970).]

As the gyral group approaches the southern part of the northern fishery area, south and southeast of the Revillagigedo Islands, the juvenile skipjack actively migrate out of the gyre into the waters around the Revillagigedo Islands and subsequently into the feeding grounds off Baja California. The cue for the start of the active migration of the juveniles out of the gyre could involve a summation of external stimuli, such as those received on encountering California Current Extension (CCE) water, coupled with internal endocrinal stimuli, such as increased thyroidal and gonadal activity. Some adults migrate with the juveniles but the majority probably remain offshore. With the southerly advance of cold water (18°-21°C isotherms) along the west coast of Baja California in late fall, the adolescent skipjack leave the area of the northern fishery (Blackburn, 1969a; Fink and Bayliff, 1970; Williams, 1970). This they do via the CCE and rejoin the gyre, although no longer dependent on it for movement, the general transport of which is in a west-southwesterly direction (NEC). The adolescent skipjack, now maturing for the first time, and the adults thus return to the spawning grounds in the central Pacific in time for the next spawning season.

With regard to timing of movements in the gyre, the only real fact is that the principal recruitment to the offshore areas of the northern fishery, the Revillagigedo Islands, lasts from about March to June, with movement to Baja California waters normally from May onwards. A continuous passive migration of young stages from long 130°W to 85°W in the NECC and then to the Revillagigedo Islands in coastal currents might take about 9-10 months (see page 753). Backtracking from the entry time at the Revillagigedo Islands would suggest movement past the meridian of 130°W from about May-June to August-September. This is close to the suggested principal spawning season, May to October, west of that meridian for the northern spawning group. The adolescent skipjack leave offshore Baja California waters principally from November to January and, even if only moving at the speed of the current (CCE, then NEC), there is adequate time to reach the central Pacific west of long 130°W by spawning time.

The time between the proposed spawning period and first entry into the offshore areas of the northern fishery is about 10-12 months and might suggest that the higher of the growth rates mentioned earlier (see page 754) is the more likely in the first year, i.e., >40 cm. With a spawning period of May to October the proposed passive transport of juveniles east of long 130°W coincides with the period when the NECC flows through to the Central American coast. When the gyre is interrupted by the breakdown of the NECC east of long 120°W from February to April, there are probably no northern group young stages to be transported eastwards.

It is proposed that the skipjack forming the southern fishery group (from which the catch is usually much greater than that in the northern fishery) spawn principally in the southern spring and summer, November to April, in the central equatorial Pacific. A large proportion of the larvae and juveniles eventually enter the NECC where development ensues during the passive migration eastwards towards the American coast (Figure 7C). As with the northern group, movements of the southern group adults would parallel the juveniles in the NECC but would be primarily in the SEC. On reaching the terminus of the NECC, the juveniles migrate actively into the offshore areas, and subsequently the feeding areas, of the southern fishery off Central and South America (mainly off Ecuador). It is difficult to suggest a specific environmental cue which may act as the external stimulus involved in triggering this change from passive to active migration. Perhaps in the southern part of the area of the NECC terminus the cue could be

related to the waters of the Equatorial Front, especially those of Peru Current origin.

The adult skipjack at this period would normally remain offshore in the eastern Pacific. When the adolescents leave the feeding grounds they, and the adults, are maturing and would move westwards in the SEC (north and south of the equator), and possibly even in the NEC, to the central Pacific spawning grounds. There is some indication from the data of Miyake (1968) that maximum occurrence of longline caught skipjack was at about lat 10°-15°S east of long 105°W, at lat 5°-10°S from long 105° to 130°-140°W, and at lat 0°-5°S west of long 130°-140°W, that is tending towards the equator away from the coast. This could be related to equatorial low temperature areas west of the Galapagos Islands.

A principal problem with a gyral model for the southern fishery group concerns the entry of larvae and early juveniles into eastbound currents. For those originating in the equatorial areas of the NEC, or the SEC north of the equator, access to the NECC through known circulatory mechanisms is relatively simple (similar to that in the passive or northern gyral migration models). For larvae and early juveniles of this group south of the equator the problem is more complex. Here the SEC has a southerly component in the westward transport tending for passively drifting animals to be carried away from the equator. For those between lat 0° and 5°S a passive movement northwards and across the equator, and hence into the NEC, could occur under the stress of unusually strong southeast or south winds, the equatorial divergence then being farther south than usual.

This problem related to skipjack young stages south of the equator raises the question of the role of the SECC in the southern gyral migration model. Migration in the subsurface SECC is improbable as mean temperatures are about 14°C (M. Tsuchiya, personal communication). However, the existence of a surface SECC, even if as narrow as 120 miles, could be of importance in completing the gyre south of the equator (see Figure 7C). Larvae south of the equator in the central Pacific would tend to be carried towards the SEC/SECC boundary, and then eastwards with it. As mentioned earlier EASTROPAC and other data showed increased "productivity" in the general region where a surface SECC might be expected (lat 10°-15°S), and this would obviously be of importance in development of the juveniles. Subsequent movement of juveniles from the surface SECC terminus would presumably be in the form of an active migration. There could also be some type of link with the Peru Countercurrent. In the southern summer adolescent skipjack often occur off northern Chile and the north-south migration route of these fish must be offshore in view of the low coastal temperatures off Peru. Fish that migrated onshore in the SECC would move, after feeding off South America, westwards in the SEC and return to the central Pacific.

Obviously timing in the two gyral migration models would be different, even though they share a common eastbound current, the NECC. When this current is flowing through to the coast, it would carry recruit skipjack of two different sizes representing the two groups. Southern fishery group recruits would be considerably larger (4-5 months older) than those of the northern group. Separation of the juveniles of the two groups at the NECC terminus would be little problem as only those of southern group origin would be in the developmental physiological state requisite to active migration. Those juveniles belonging to the northern group would continue their passive migration. Intermingling of groups could occur if some northern group juveniles were passively carried into southern fishery areas especially off Central America.

As in the passive migration model (see page 753), to account for the size differences in incoming recruits, one would have to propose that: the southern group spawning grounds are farther west than those of the northern group, and/or the transfer mechanisms involved in the movement of young stages into eastbound currents are complex and take longer (certainly true if no SECC). Either or both of these proposals could account for southern group juveniles, spawned November to April, not reaching the area of long 130°W at the time when the NECC has stopped east of that meridian. Alternatively, if juveniles from the southern spawning group

(southern fishery group) were somehow retained west of long 130°W from February to April, when the NECC is stopped, then this would reduce the apparent distance westward from the coast that the entry times to the southern fishery would otherwise imply.

The existence of a surface SECC would certainly facilitate the recruitment of juvenile skipjack (of southern origin) into the southern fishery. However, one would expect such a current to be highly variable in space and time, and hence such recruitment would be similarly affected.

GENERAL COMMENTS AND RECENT RESEARCH

An active migration of juvenile skipjack from the central to the eastern Pacific would be categorized as a "between habitat migration," using the definition of Nakamura (1969). Similarly with the gyral migration models, the active migration of juveniles from the gyres to the feeding grounds would fit this definition. This type of migration, Nakamura suggested, takes place following a change in ecological state, for which one might perhaps synonomize developmental physiological state. Nakamura also hypothesized that "between habitat migrations," which entail changes in environment (current systems, water masses), occur principally at the equinoxes, about March in the northern hemisphere and September in the southern hemisphere, and that the movements are rapid and on a large scale. In the eastern Pacific the principal recruitment into the offshore areas of the northern fishery starts about March and lasts to about June; there is also some recruitment about October (± 1 month). However, recruitment to the offshore areas of the southern fishery appears to be over a considerably longer period, November to April, and perhaps from as early as August (± 1 month).

The Bureau of Commercial Fisheries (now the National Marine Fisheries Service), Honolulu, undertook five quarterly cruises, from May 1969 to May 1970, between lat 12°N and 3°30′S along the meridian of long 145°W, to consider the distribution and abundance of skipjack in the equatorial current systems. Preliminary data from these cruises (Walter M. Matsumoto, personal communication) show longline skipjack catches were generally low except in the area of the NECC (lat 7°30′N), where they were relatively high in the first and fourth quarters (February and October-November). Trolled catches of skipjack on the last three cruises were variable but consistently high in the NECC. Catches by both methods were lowest at the equator in the vicinity of the EUC. Catches of juvenile skipjack made with a midwater trawl were relatively high in the SEC at lat 3°30′S through most of the year, while catches in the NECC peaked in the second and third quarters (May and June). Plankton hauls (1-m net) showed largest catches of larvae were made in the SEC just south of the NECC.

These results suggest that skipjack north of the equator spawn in the second and third quarters, or even slightly earlier, and that the juveniles are concentrated in the NECC at this time. The high year-round abundance of juveniles at lat 3°30′S apparently indicates either sequential seasonal spawning of the northern and southern groups or continual equatorial spawning of a single group. Richard A. Barkley and Richard S. Shomura (personal communications) have previously suggested that the shallow EUC could be involved in the eastward transport of skipjack young stages. At least east of long 120°W this seems unlikely as even in the upper regions of the EUC temperatures (18°-20°C) are marginal for adult skipjack let alone larvae. Even in the vicinity of the EUC at long 145°W, where temperatures may be about 20°C, the lack of juveniles and adults would appear to confirm this finding.

Hida (1970) reported on an exploratory fishing cruise for tuna made by the Bureau of Commercial Fisheries, Honolulu, in October-November 1969 concentrated in the area, lat 6°N-8°S, long 115°-125°W. Surface schools of tuna fishable by pole-and-line were found from lat 2°-5°N (just south of the NECC); skipjack predominated in the catches, though some large schools consisted of yellowfin, bigeye, or all three mixed. The skipjack, caught by this method and trolling, ranged from 45 to 79 cm FL (means 47-68 cm) and gonads were maturing or mature (only one

spent). Only one school of small skipjack was fished by pole-and-line, at lat 4°S, and the fish were from 36 to 51 cm (mean 40 cm). However, enroute to and from Hawaii (lat 10°N-5°S, long 125°-145°W) troll catches of skipjack were mainly of small fish, <45 cm. The data from this cruise add little to the proposed migration models except to indicate the wide geographic range of recruit size skipjack west of long 125°W in October-November 1969. In addition, east of long 125°W fish were in the medium to large category and in schools large enough to be fished successfully by a commercial method—live bait pole-and-line. None of these fish had recently spawned.

Williams (1971) described plans for a series of eight cruises, initiated by the NMFS, La Jolla, and the Scripps Tuna Oceanography Research (STOR) Program, to investigate the distribution of skipjack in relation to environmental conditions in two offshore areas of the eastern Pacific. The two areas, (A) lat 15°N-5°S, long 115°-125°W, and (B) lat 5°N-15°S, long 95°-115°W, were considered the most important for testing migration models for skipjack, including the three now proposed for recruits.

The first cruise (two vessels) was to Area A in October-December 1970, with trolling as the principal fishing method. Recruit size fish ($\leqslant$40 cm) were found in the NEC some distance to the north of the NECC, as well as immediately to the north and south of the NECC. Large fish were widely distributed, but with fewest found in the NECC and most in the section of the SEC north of the equator. About 27% of the fish $\geqslant$45 cm, the gonads of which were examined, were found to be in a spent or spent-recovering condition; most were found in or close to the NECC, and none south of the equator. A first sorting of midwater trawl samples showed no skipjack juveniles; data on occurrence of larvae are not yet available.

The second cruise to the same area, in March-April 1971, caught few small fish and none <40 cm. More large fish were caught north of the equator than on the previous cruise. The presence of a surface NECC, even though weak and narrow (180-120 miles wide), at this time of year and at this meridian was anomalous. About 60% of the fish examined had gonads in a recovering state and were from all current systems north of the equator.

The results of these two cruises confirm that some skipjack spawn in the equatorial zone not too distant from long 120°W. Those fish taken in March-April 1971 appeared to have gonads in a more advanced state of recovery than most taken in October-December 1970 (subjective analysis). Presence of these spent and spent-recovering fish could indicate support for the gyral migration models, where it is proposed that after spawning west of long 130°W adults move eastwards paralleling the movement of the young stages. However, even with the active and passive migration models there could be small-scale diffusion movements of adults out of the central Pacific (including east of long 130°W) subsequent to spawning. The appearance of spent and spent-recovering gonads in October-December skipjack suggests they were of northern summer spawning origin, while the recovering gonads in March-April fish rather indicate southern summer spawners; or alternatively that spawning in skipjack is truly a year-round function in the equatorial zone. The apparent absence of juveniles in the trawl hauls may be due to ineffective sampling gear. The presence of very small fish (<40 cm) in areas of high forage concentrations at the NECC boundaries, as well as in the NEC somewhat further north, would tend to support the active migration models. They could be either some of the last recruits destined for the southern fishery or early ones for the northern fishery; their presence in the NEC as far north as lat 13°N, and size (30-40 cm) suggests the latter. The significance of the shift in the center of apparent abundance of large fish from lat 1°-5°N to 9°-11°N between October-December and March-April is not yet apparent.

A further six cruises, starting with one to the southern area (B) in August-October 1971, are planned. Data from this series of cruises will undoubtedly increase our ability to describe, particularly for offshore areas, the distribution, apparent abundance, life history, and environment of the skipjack. Although input of these data will be valuable in preparing models, such as

those of migrations, there is also a need for a greater input related to the physiology, behavior, and genetics of the species than is presently available.

The hypothetical nature of certain aspects of the proposed models of skipjack migrations advanced here cannot be denied. However, at this stage in the development of research on the skipjack resources of the central-east Pacific, a presentation of existing data and ideas on skipjack migrations, in the form of models, appears fully justified. Indeed present research plans were formulated on the basis of the active migration model (the first proposed), although they are equally applicable to testing the other models as well.

With any of the proposed migration models it is obvious that oceanographic conditions in the central-east Pacific will have a vital controlling effect on the subsequent abundance of skipjack in the eastern Pacific fishery. First, through year-class strength of recruits (spawning success/larval survival) and second, through the number of recruits actually entering the fishery (migration success). Not only is it necessary to test the mechanisms of these, and other, migration models, but monitoring and more detailed analyses of inter- and intraseasonal fluctuations in the central-east Pacific environment will assist in understanding, and perhaps in predicting, the fishery-independent changes in skipjack apparent abundance.

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HAWAIIAN-CAUGHT SKIPJACK TUNA AND THEIR PHYSICAL ENVIRONMENT

GUNTER R. SECKEL[1]

ABSTRACT

Empirical associations between the occurrence of skipjack tuna (*Katsuwonus pelamis*) in Hawaiian waters and environmental conditions point to the current system as an important cause for the variations in the Hawaiian fishery. Large interyear differences of sea-air interactions in the skipjack spawning areas may affect larval survival and year-class strength. A numerical drift model was used to investigate the contribution of currents to the travel of skipjack from the eastern North Pacific to Hawaii. Floating objects introduced in the model ocean at long 120°W and lat 10° to 20°N converge toward the northern edge of the North Equatorial Current near Hawaii in 21 to 23 months. The time of freedom of skipjack tagged in the eastern North Pacific and recovered in Hawaiian waters is of the same magnitude. It is concluded that for skipjack a possible mode of travel from the eastern North Pacific to Hawaii is drifting in the North Equatorial Current. The variability in abundance and size-frequency distributions observed in the Hawaiian fishery can be caused by changes in the current system. Numerical models of the type presented can be verified and so permit progress from the exploratory to the experimental phase in fisheries investigations.

Over a decade ago empirical associations were established between environmental parameters and the availability of skipjack tuna (*Katsuwonus pelamis*) to the Hawaiian fishery. Since that time oceanographic studies have provided additional information to augment these associations that can now be used to postulate causal relationships. Such hypotheses are an essential step in bringing ecological studies from the exploratory to the experimental phase, numerical analysis, and, eventually, prediction.

In this paper I will briefly review the empirical associations that were established and introduce new information that has resulted from the Trade Wind Zone Oceanography investigation. The empirical associations lead to two environmental processes that must be included in numerical models describing the distribution of skipjack. One concerns the sea-air interaction processes that may affect productivity and larval survival, and the other concerns the current field that affects the distribution of skipjack schools. The latter is illustrated by a numerical "drift model" for a portion of the Pacific North Equatorial Current.

The purely physical explanations that are given for the varying availability of skipjack in the Hawaiian fishery and the implications of the drift model results may conflict with beliefs based on biological considerations. Such conflicts can be resolved if the proposed hypotheses are tested experimentally as suggested in this paper.

It is fitting that this work should be reported in Dr. Sette's Festschrift. He provided great impetus and leadership to the integration of environmental studies with fisheries research. The work on Hawaiian-caught skipjack and on their environment was initiated at the time Dr. Sette directed the Pacific Oceanic Fishery Investigations (POFI) in Hawaii.

REVIEW OF EMPIRICAL ASSOCIATIONS

THE HAWAIIAN SKIPJACK FISHERY

The Hawaiian skipjack fishery has been described by Yamashita (1958) and Uchida

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(1966). Landings from this fishery range from about 91 tons[2] (200,000 lb) per month in February to more than 907 tons (2 million lb) per month in July. Total annual landings also show wide variations ranging from 2,676 tons (5.9 million lb) as in 1969 to 7,302 tons (16.1 million lb) as in 1965.[3] Hawaiian fishing vessels fish within sight of land, mainly in the vicinity of the islands of Oahu to Maui and Hawaii (Uchida, 1970). Thus, Hawaiian skipjack landings provide, in contrast to other fisheries where fishing fleets may follow the fish concentrations, a time sequence measure from a fixed area.

Uchida (1967) analyzed the catch and effort in the Hawaiian fishery and found that although there has been a decline in the number of vessels fishing on a full-time basis during the last 15 years, there is no clear evidence that this decline has affected total landings. It appears that the decline in the number of fishing vessels occurred primarily among the smaller boats (Uchida 1966: Table 6) and, also, that the decline was offset by increased efficiency of fishing. For purposes of this paper, it is important to note that the large fluctuations in total annual landings are also reflected by the average annual catch per standard effective trip (Uchida, 1967: Figure 8). The annual landings of skipjack, therefore, reflect availability near Hawaii.

THE OCEAN ENVIRONMENT NEAR HAWAII

The oceanographic climate of the Hawaiian Islands region was described by Seckel (1962). Of interest are the North Pacific Central and the North Pacific Equatorial water types and the transition water of the California Current Extension between these water types (Figure 1). Seckel (1968) defined the North Pacific Central water as that with a salinity of more than 34.8‰ and the North Pacific Equatorial water as that with a salinity of less than 34.2‰. These salinities are always found in the salinity gradients that actually define the water type boundaries.

The boundary of the North Pacific Central water lies near the Hawaiian fishing area and is displaced north-southward both seasonally and nonseasonally. Usually the boundary lies just south of the islands in fall and winter and within or north of the islands during spring and summer. The boundary displacement is reflected by the salinity as measured at Koko Head, Oahu (Seckel and Yong, 1971). Low salinities occur during spring and summer and high salinities during fall and winter. During some years, such as in 1957 and 1958, the islands were bathed in North Pacific Central water throughout the year and in 1968 the islands were bathed in the transition water of the California Current Extension throughout the year.

The large effect of heat exchange across the sea surface tends to obscure the effect of advection on the sea-surface temperature. Nevertheless, the change of temperature due to advection is apparent in graphs of the change of temperature per month (Seckel, 1962). Warm advection in late winter and early spring causes the temperature in Hawaiian waters to rise before it would rise due to the onset of seasonal heating across the sea surface. The temperature increases and the salinity decreases southward near Hawaii. Warm advection is therefore associated with a northward component of flow that also causes a decline in the salinity.

Extremes of temperature and salinity as observed at Koko Head, Oahu, range from about 22.5°C in February or March to 27.4°C in September or October and from 34.4‰ in July to 35.5‰ in late fall or early winter. Inorganic phosphate concentrations in the Hawaiian region as well as in the North Equatorial Current are about 0.3 μg at./liter. Seasonal variations have not been observed.

In the Hawaiian region 10 to 40 cc of zooplankton per 1,000 m^3 of water are filtered by a 1-m net in 200-m oblique tows (King and Hida, 1954, 1957a, 1957b; Nakamura, 1967). King and Hida (1954: Figure 16) indicate that an average zooplankton volume of about 25 cc per 1,000 m^3 of water filtered near Hawaii compares with 20 to 25 cc in the North Equatorial Current and with about 38 cc near the equator to the south of Hawaii. There is no clear indication of a sea-

[2] Metric tons are used throughout this paper.
[3] Source: Hawaii State, Division of Fish and Game.

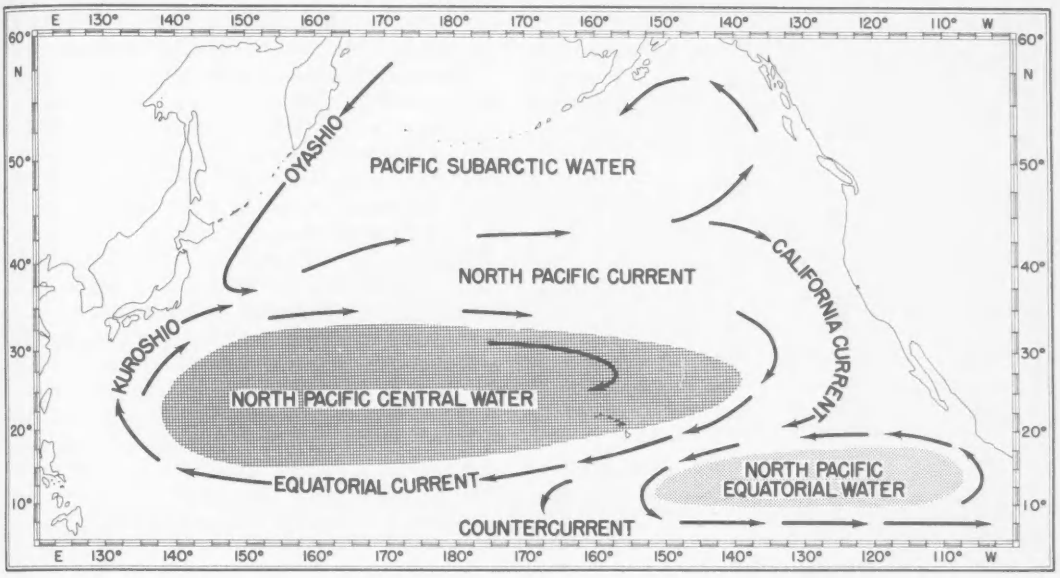

FIGURE 1.—Schematic chart of the major North Pacific water types and currents.

sonal variation in zooplankton concentrations in Hawaiian waters but longer term variations appear to take place. There has been no systematic sampling of tuna forage by midwater trawls.

SKIPJACK AND THE ENVIRONMENT

Blackburn (1965) summarized the range of environmental conditions within which skipjack are known to exist. The conditions summarized in the previous section fall well within this range. The seasonal changes in the Hawaiian environment are therefore not the probable cause for the variations in skipjack availability. Inorganic phosphates, as possibly affecting primary productivity, or the concentration of zooplankton vary insufficiently to explain a tenfold increase in catch rates during the summer months.

It is common to think of temperature and salinity changes in terms of their physiological effect on the biota. These changes, however, also reflect dynamic properties of the environment such as heat exchange across the sea surface and advection that, in turn, affect biological distributions. Thus, when temperature and salinity changes were used in the Hawaiian region as indices of heat exchange and advection (Seckel, 1962) associations between the dynamic properties of the environment and the availability of skipjack became apparent. Development of the empirical associations and their implications can be traced in Seckel and Waldron (1960), Murphy, Waldron, and Seckel (1960), Seckel (1962), U.S. Bureau of Commercial Fisheries (1963).

It was found that the seasonal intrusion of the California Current Extension water into the Hawaiian region, as reflected by the surface salinity, coincides with the seasonal increase in the availability of skipjack. To monitor this association, the salinity measured at Koko Head, Oahu, during July can be used as an index of the water type during the peak of the fishing season.

The northward component of flow during late winter and early spring that causes the displacement of North Pacific Central water by California Current Extension water near Hawaii, also causes warm advection. It was found that strong or early warm advection as reflected by

TABLE 1.—Annual landings of skipjack in Hawaii, 1952-1970, with time of initial warming and mean July salinities of sea-surface water.

Year	Time of initial warming[1]	July mean salinity (‰)[1]	Total landings 10^3 metric tons
1952	March	>34.8	3.31
1953	February	<34.8	5.47
1954	February	<34.8	6.36
1955	March	<34.8	4.40
1956	February	34.72	5.05
1957	March	34.98	2.78
1958	March	34.87	3.10
1959	February	34.73	5.63
1960	March	34.69	3.34
1961	February	34.77	4.94
1962	March	34.86	4.27
1963	February	34.84	3.67
1964	March	34.82	4.09
1965	February	34.67	7.33
1966	March	35.01	4.26
1967	January	34.83	3.65
1968	January	34.50	4.23
1969	February	34.72	2.71
1970	March	34.98	3.33

[1] Time of warming and July salinities are based on observations at Koko Head, Oahu, except 1952 to 1955 when they are based on observations irregularly made in the vicinity of Oahu.

initial warming occurring before the end of February precedes favorable fishing conditions. Weak or late warm advection is reflected by initial warming in March and precedes unfavorable fishing conditions.

The empirical associations are summarized in Table 1, giving the time of initial warming (temperature index), the mean July salinity, and the annual landings of skipjack in Hawaii. The indices are based on measurement, regularly made at Koko Head, Oahu, since November 1955. Indices between 1952 and 1955 are estimates based on sea-surface temperature and salinity observations irregularly made in the vicinity of Oahu. Prior to 1952 there were insufficient data to make estimates.

When the associations between availability of skipjack and time of initial warming were first established, monthly mean temperatures were used. Now Koko Head temperatures are expressed by harmonic functions of time (Seckel and Yong, 1971). These functions have been used to determine objectively the time of initial warming given in Table 1. Formerly, a salinity of 35‰ was used to indicate the boundary between North Pacific Central and California Current Extension waters. Here, in keeping with the definitions given by Seckel (1968), a salinity of 34.8‰ has been used to indicate this boundary.

The temperature and salinity indices can each be assigned a rating of favorable (F) or unfavorable (U) for fishing. There are therefore three categories according to which the landings are classified and shown in Figure 2a: Both indices favorable (FF), one unfavorable (FU or UF), and both unfavorable (UU).

The 1968 and 1969 landings did not fall within the FF range of previous years. Examination of environmental conditions revealed that during these years minimum salinities were the lowest recorded since the sampling series began at Koko Head, Oahu (Seckel and Yong, 1971). A sharp drop in values took place in late winter 1968 and the salinity remained low until late summer of 1969 when values rose to a normal level. Minimum salinities occurred in June 1968 and May 1969 and averaged 34.49‰ and 34.59‰, respectively. This information, as well as that to be introduced in the next section, indicates that favorable "skipjack water" is confined to the high-salinity portion of the California Current Extension. For favorable fishing conditions, therefore, the additional constraint is introduced that mean monthly salinities during spring must be above 34.6‰. With this new constraint, landings for 1968 and 1969 fall into the FU category (Figure 2b).

Of the 19 years for which skipjack landings in Hawaii can be associated with environmental conditions, 6 years fall in the FF category, 7 in the UU category, and 6 in the FU category when the revised salinity index is used. Figure 2b illustrates that there is a clear separation between the landings in the FF category on the one hand and the FU and UU categories on the other. The average annual landings are 5,800 tons, and 3,700 tons and 3,600 tons in the FF, FU, and UU categories, respectively. The lowest value in the FF category (4,900 tons) is higher than the highest value in the FU category (4,400 tons) or in the UU category (4,300 tons). The 19-year average of annual landings was 4,300 tons.

Annual landings, therefore, can be classified into two groups. One group comprises the landings in the FU and UU categories that average 3,600 tons and range from 2,710 to 4,400

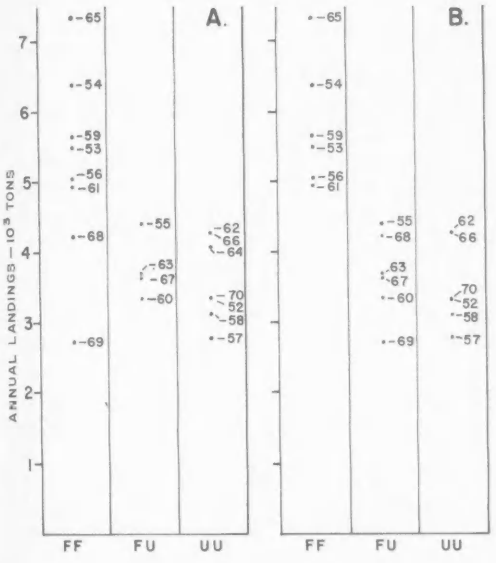

FIGURE 2.—Annual skipjack landings in Hawaii grouped according to the temperature and salinity indices being both favorable, FF, one favorable and the other unfavorable, FU, and both unfavorable, UU. Panel A: Salinity index is favorable with July salinity less than 34.8‰. Panel B: Salinity index is favorable with July salinity less than 34.8‰ but spring salinity higher than 34.6‰.

tons. The other group comprises the landings in the FF category that average 5,800 tons and range from 4,940 to 7,330 tons. Landings in the first group occur two-thirds of the time and are normal for Hawaii. Landings in the latter group are clearly exceptional.

Into which of the two groups landings will fall is in part predictable. The temperature index is determined in April, well before the beginning of the summer fishing season. The salinity, however, is monitored during spring and has little predictive value. During the 19 years under consideration there have been 4 years when the temperature index was favorable but the salinity was unfavorable. Two of these years were 1968 and 1969, when the spring salinity was the lowest recorded at Koko Head. Thus, the temperature index can be used to predict the exceptional fishing years in four out of five cases. This predictability can be improved by subjective interpretation of the salinity trends prior to the fishing season.

SKIPJACK AND THE TRADE WIND ZONE OCEANOGRAPHY RESULTS

In the Trade Wind Zone Oceanography (TWZO) investigation, oceanographic stations were occupied at fixed locations between lat 10° and 26.5°N along long 148°, 151°, 154°, and 157°W at approximately monthly intervals from February 1964 to June 1965 (Figure 3). Although

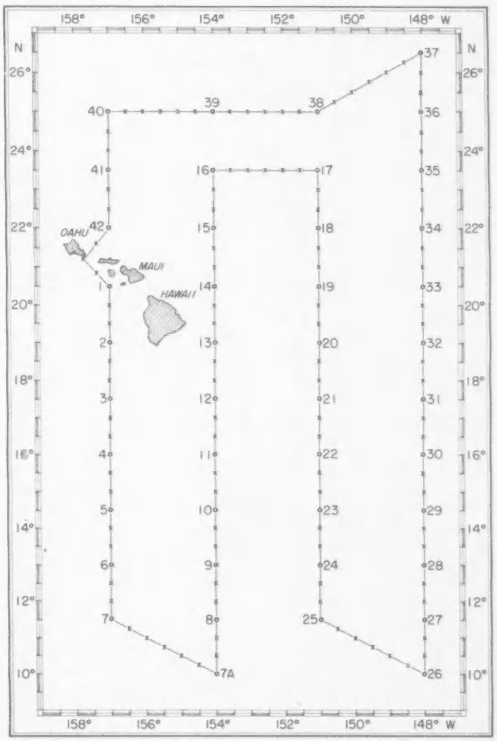

FIGURE 3.—Track of the Trade Wind Zone Oceanography cruises. Numbered circles indicate oceanographic stations.

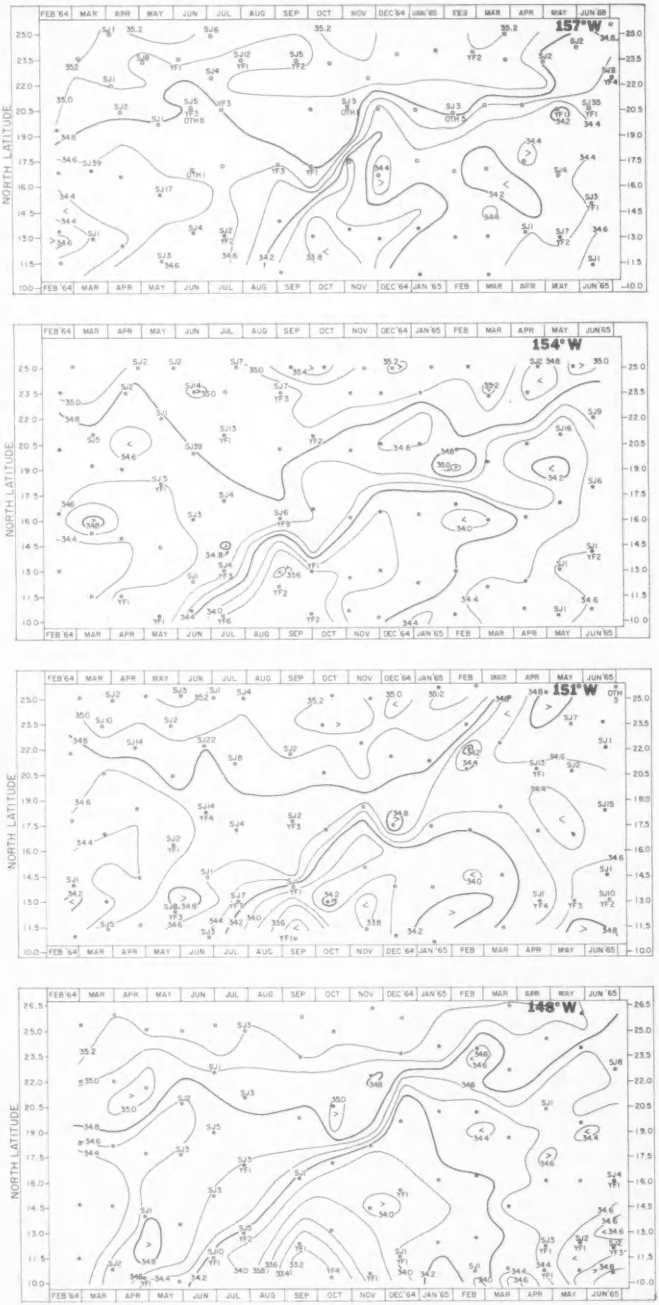

FIGURE 4.—Salinity (‰) distribution at 10 m, lat 10° to 26°N, long 148°, 151°, 154°, and 157°W, February 1964 to June 1965. Small circles indicate location of plankton tows. The number of skipjack (SJ), yellowfin (YF), and other tunalike larvae (OTH) captured are shown.

no fishery studies were undertaken to complement the oceanographic studies, results of the TWZO investigation augment the associations between skipjack and the environment that were described above. During each of the cruises, which lasted about 20 days, ½-hr plankton tows were made every evening between 8 and 9 o'clock with a 1-m net just below the sea surface. From each of the 19 or 20 plankton samples per cruise the tuna larvae were separated and identified.[4]

The descriptive results of the TWZO investigation have been summarized by Seckel (1968). Figure 4 shows the time variation in the meridional, 10-m salinity distribution for long 148°, 151°, 154°, and 157°W. The positions of the plankton tows and the number of skipjack, yellowfin or other tunalike larvae are superimposed on these graphs. The salinity isopleths 34.8‰ and 34.2‰ are drawn heavier to demark the southern boundary of the North Pacific Central water and the northern boundary of the North Pacific Equatorial water, respectively.

Along the meridian 157°W that passes through the Hawaiian Islands, the seasonal northward displacement in the spring of 1964 of the North Pacific Central water is evident. Subsequent southward retreat was stopped when a sharp northward displacement took place in October and November. Another sharp northward displacement of the 34.8‰ salinity isopleth took place in May. A pronounced feature along all meridians presented is the intrusion of the North Pacific Equatorial water during the spring and summer of 1964.

The TWZO observations spanned the entire 1964 and the beginning of the 1965 fishing seasons in Hawaii. With landings of 4,093 tons, 1964 fell into the normal category of fishing years (Figure 2b). Landings of 7,329 tons, in 1965, however, were the best on record and fall into the exceptional year category. The salinity distribution along long 157°W shows an important year-to-year difference in the meridional salinity gradient. During the winter and spring of 1964 the gradient was small or diffuse. During the winter and spring of 1965 the gradient was pronounced or high. Qualitatively, the differences in meridional gradients means that the currents were only weakly convergent in 1964 in contrast to the strong convergence or shear that existed in 1965.

This interpretation provides an additional lead towards an understanding of the association between the availability of skipjack and the environment. The concentration of organisms, whether drifting with the water, such as plankton, or swimming relative to the water, such as skipjack, is affected by water motion. Thus, the strongly convergent flow pattern evident from the high-salinity gradient would concentrate the skipjack schools and so increase their availability, unless, of course, the effect of the convergent flow is deliberately opposed. The concentrating effect is evident in Figure 5 showing the weekly skipjack landings in Hawaii and the Koko Head salinities. The sharp drop in Koko Head salinity at the beginning of May 1965 is coincident with the movement of the salinity gradient through the fishing area (Figure 4) and with the pronounced increase in weekly landings. A similarly pronounced change in landings with change in salinity was reported by Murphy et al. (1960).

Consider now the distribution of skipjack

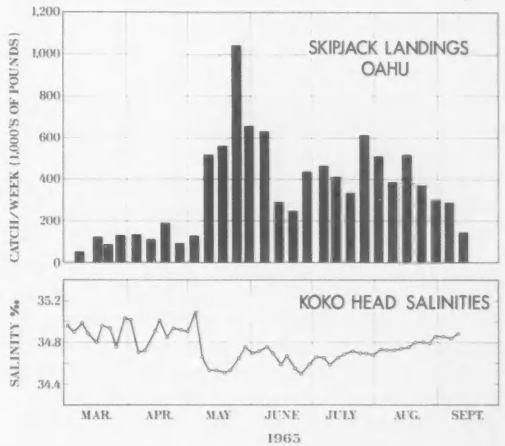

FIGURE 5.—Weekly skipjack landings at Oahu, March to September 1965 (upper panel), and Koko Head salinities (lower panel).

[4] The identifications of tuna larvae were made by Walter M. Matsumoto of the National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory.

larvae shown in Figure 4. The size of skipjack larvae caught in plankton nets such as were used in the TWZO investigation range from 2.3 to 20.1 mm (Matsumoto, 1958). During the first month, growth is rapid and larvae may reach a length of 9 cm (Yoshida, 1971). Thus, presence of larvae indicates recent presence of adults. Only the presence or absence of larvae in a tow is considered, and tows with different larvae counts are not distinguished. General absence of larvae as between October 1964 and April 1965 may mean absence of adults or cessation of spawning. During the spring and summer of 1964 and spring of 1965, skipjack larvae, and therefore adults, occurred in all latitudes sampled during the TWZO cruises. The distribution, however, was not uniform. There were only few tows that captured larvae in water with a salinity above 35‰ and none in water with a salinity of less than 34‰.

Remembering that the salinity is used as an index of water type, the total number of plankton tows and the number of tows with skipjack larvae are listed in Table 2 as a function of salinity. The highest number of tows with skipjack larvae occurred in a salinity range from 34.61 to 34.8‰. Although there were 23 tows in water with a salinity below 34‰, no skipjack larvae were captured. The percentage of tows with larvae as a function of salinity is shown in Figure 6. The highest capture rate, 60%, occurred in water with a salinity of 34.61 to 34.8‰.

Quantitative sampling for tuna larvae is difficult and results must be interpreted with caution. However, during February to June of 1964 and 1965, 97 and 95 plankton tows were made, respectively. For all tows the same sampling procedures were followed. Interyear comparisons of the larvae capture rates, therefore, provide additional leads in gaining an understanding of the environment-skipjack relationship.

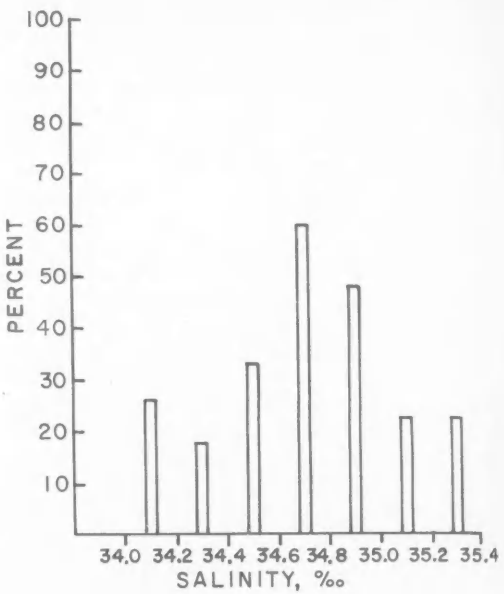

FIGURE 6.—Percent of plankton tows with skipjack larvae as a function of salinity from Trade Wind Zone Oceanography cruises, February 1964 to June 1965.

It is evident from Figure 4 that there were fewer tows with skipjack larvae in 1965 than there were in 1964. The number of tows with larvae and the total number of tows are listed in Table 3 for the cruises from February to June of each year as a function of salinity. With almost the same number of tows in each case, those with larvae in 1964 numbered 45 and those in

TABLE 2.—Summary of plankton tows with and without skipjack larvae as a function of salinity for all the Trade Wind Zone Oceanography cruises, February 1964 to June 1965.

Salinity Range ‰	33.01 –33.2	33.21 –33.4	33.41 –33.6	33.61 –33.8	33.81 –34.0	34.01 –34.2	34.21 –34.4	34.41 –34.6	34.61 –34.8	34.81 –35.0	35.01 –35.2	35.21 –35.4	35.41 –35.6	Total
Number of tows with skipjack larvae	0	0	0	0	0	6	7	18	34	21	9	5	0	100
Total number of tows	1	2	0	7	13	23	39	54	57	44	40	22	3	305

TABLE 3.—Summary of plankton tows with and without skipjack larvae as a function of salinity for the Trade Wind Zone Oceanography cruises, February to June 1964 and February to June 1965.

Salinity Range ‰		33.81 –34.0	34.01 –34.2	34.21 –34.4	34.41 –34.6	34.61 –34.8	34.81 –35.0	35.01 –35.2	35.21 –35.4	35.41 –35.6	Total
February to June 1964	Number of tows with skipjack larvae		2	2	3	16	12	5	5		45
	Total number of tows		2	11	16	26	17	13	12		97
February to June 1965	Number of tows with skipjack larvae		1	4	13	11	3				32
	Total number of tows	1	7	22	29	18	9	8	1		95

1965 numbered 32. This comparison is consistent with that made by Yoshida (1971) of the relative number of skipjack larvae found in billfish stomachs. The number of juveniles per 100 billfishes taken in 1964 was 21.3 and in 1965 the juveniles numbered 19.1.

The relative number of tows with larvae as a function of salinity for each year is shown in Figure 7. In 1964, although the total number of tows with larvae was highest in the 34.61 to 34.8‰ water, the highest capture rate was in 34.81 to 35.0‰ water. In 1965 highest capture rates were shifted to lower salinities. The highest percentage of tows with larvae, 60%, occurred in water with salinities of 34.61 to 34.8‰. The restrictions placed on the salinity index in the previous section is consistent with the capture rates of larvae during the TWZO cruises.

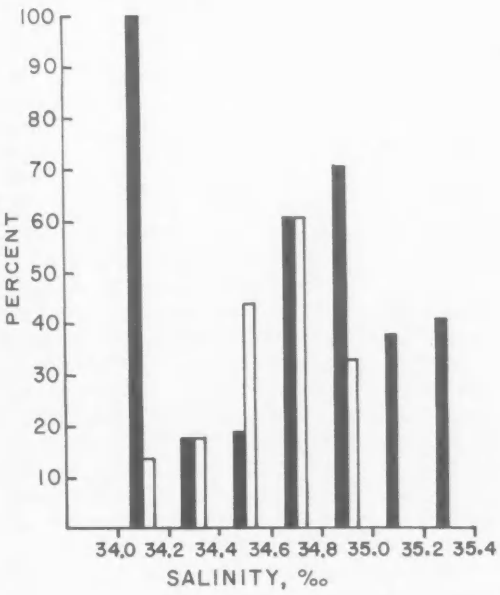

FIGURE 7.—Percent of plankton tows with skipjack larvae as a function of salinity from Trade Wind Zone Oceanography cruises, February to June 1964, solid bars, and February to June 1965, open bars.

It seems paradoxical that during 1965, the year with the highest skipjack landings in Hawaii, the number of tows with larvae (reflecting presence of adult skipjack) was lower than in 1964. Figure 7 shows that larvae were spread over a wider range of salinities in 1964 than in 1965, the difference occurring between 35 and 35.4‰. Although there were fewer tows in the high-salinity water during 1965 than during 1964, assuming the same capture rate as in 1964, there should have been three or four tows with larvae in the 35 to 35.4‰ salinity range during 1965. Thus, there were possibly as many or more skipjack in 1964 than in 1965 but their concentration was lower in 1964 resulting in lower Hawaiian landings. This picture is consistent with the salinity distribution, which had a high meridional gradient in 1965 as compared to 1964, reflecting stronger convergence.

Another possible cause for the difference in capture rates of larvae between 1964 and 1965 was recognized early in this century. Hjort (1914) suggested the possibility that the availability of food at the time of yolk absorption is

critical for the survival of larvae. In a large portion of the tropical and subtropical oceans food supply (plant production) may be governed by sea-air interaction processes. During the TWZO investigation there were large differences in sea-air interactions between the early parts of 1964 and 1965 (Seckel, 1970a,b). As an example, the heat of evaporation, $Q(E)$, the net heat exchange across the sea surface, $Q(N)$, and the zonal component of the wind stress, $\tau(x)$, for lat 17°N, long 152°W are listed in Table 4. The

TABLE 4.—Interyear differences of the heat of evaporation, $Q(E)$, the net heat exchange across the sea surface, $Q(N)$, and the zonal component of wind stress, τ_x, lat 17°N, long 152°W. $Q(E)$ and $Q(N)$ are positive if the sea gains heat, τ_x is positive to the east. (Seckel, 1970a,b.)

	$Q(E)$ cal cm^{-2} day^{-1}	$Q(N)$ cal cm^{-2} day^{-1}	τ_x dynes cm^{-2}
Jan-Apr 1964 average	−441	−44	−1.71
Jan-Apr 1965 average	−134	100	− .76
Interyear difference	307	144	.95

evaporation rate in January to April of 1964 was almost three times as large as during the same months of the following year. The sea-surface layer gained an average of 144 cal cm^{-2} day^{-1} more heat during the early part of 1965 than it did during the same time of 1964. The wind stress was more than twice as strong in 1964 than in 1965. Such interyear differences take place throughout the spawning areas of skipjack. For example, the large year-to-year temperature variations at Christmas Island (Seckel and Yong, 1971) reflect large changes in sea-air interaction processes.

IMPLICATIONS OF ENVIRONMENTAL ASSOCIATIONS

THE DRIFT HYPOTHESIS

The pronounced salinity gradient at the boundary of the North Pacific Central water in 1965 (Figure 4) implies strong convergence. Organisms drifting or skipjack schools swimming in the converging currents also converge into the boundary region. The availability of fish is therefore expected to be larger within than outside of the zone of convergence. Interyear differences in the intensity of convergence as reflected by the meridional salinity gradient in the springs of 1964 and 1965 contribute to the interyear differences in availability. The boundary or convergence zone need not remain at the same location and may shift northward as indicated by the low Koko Head salinities during 1968 and 1969. Consequently, fish concentrations were also shifted out of the Hawaiian fishing grounds resulting in the low landings for these years.

The convergence of skipjack schools concept can be applied on a broader scale. Rothschild (1965) postulates that a component of Hawaiian-caught skipjack originates in the eastern Pacific. This hypothesis is supported by the recapture of fish in Hawaiian waters that were tagged in the eastern Pacific (Table 5).[5] Consider now skipjack schools that entered the North Equatorial Current in the eastern Pacific. Throughout the time while the skipjack schools are carried westward by the current, they are also displaced northward by a meridional component of the trade wind-driven surface current. The magnitude of the mean annual westward component of wind stress long 120° to 160°W between lat 10° and 25°N (University of California, 1948) is shown schematically with the associated northward component of the wind-driven surface current in Figure 8. Under these wind conditions an object would take on average about 22 months to drift from lat 10° to 20°N.

Figure 8 also shows that the northward wind-driven current decreases with increasing latitude. The number of skipjack schools drifting from the 10°-15° into the 15°-20° latitude band is larger than the number drifting from the 15°-20° to the 20°-25° latitude band. In other words, schools in the North Equatorial Current would converge north of lat 15°N.

These qualitative considerations can be expressed numerically. The displacement of a fish school, S, during a time interval, Δt, is

[5] Tagging data were kindly supplied by Dr. William H. Bayliff, Inter-American Tropical Tuna Commission.

$$\Delta S = V\Delta t.$$

The velocity of the fish school, V, consists of two parts: the velocity of the water relative to fixed coordinates, V_W, and the velocity of the school relative to the water, V_F. The displacement equation is

$$\Delta S = (V_W + V_F)\ \Delta t.$$

The velocities are functions of location and of time and the net displacement of a school after a time T is

$$S = \sum_{i=1}^{n} [(V_W + V_F)\Delta t]_i$$

or

$$S = S_W + S_F = \sum_{i=1}^{n} (V_W\Delta t)_i + \sum_{i=1}^{n} (V_F\Delta t)_i$$

with $T = n\Delta t$ if the time increments are all equal.

Although this displacement equation is true for any time and space scale, current or swimming velocities averaged over time intervals, Δt, of a week or a month are of interest here. Random motions of fish schools and eddying currents therefore make no contribution to the net displacement in the scales under consideration. It is evident that in migrations of thousands of kilometers taking a time of 1 to 2 years, ocean currents cannot be ignored unless

$$V_W << V_F$$

and the displacement of the school due to the current, S_w, is therefore small compared to that relative to the water.

If the environmental conditions are known, then a numerical integration can be performed to determine the displacement of a fish school caused by currents alone. An example of a drift model that is applicable to skipjack originating in the eastern North Pacific will be given in a subsequent section.

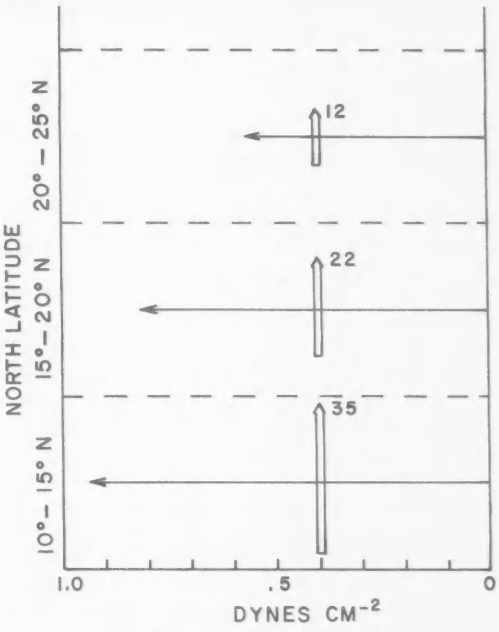

FIGURE 8.—Schematic presentation of average zonal wind stress, long 120° to 160°W, in latitude bands 10°-15°N, 15°-20°N, 20°-25°N, and associated meridional component of wind-driven current in miles per month (thick arrows).

TABLE 5.—Skipjack tagged in the eastern Pacific and recaptured in the central Pacific.

Tag release		Tag recapture		
Date	Area	Date	Area	Days free
17 Apr. 1960	Revillagigedo Is.	22 Aug. 1962	Hawaii	858
5 Sept. 1960	Baja California	12 June 1962	Hawaii	646
22 Sept. 1961	Baja California	5 Apr. 1963	Christmas Is.	561
5 June 1965	Revillagigedo Is.	27 June 1967	Hawaii	753
6 Nov. 1969	Clipperton Is.	21 July 1970	Hawaii	258
6 Nov. 1969	Clipperton Is.	8 Aug. 1970	Hawaii	276
26 Oct. 1969	lat 4°11'N, long 119°02'W	14 July 1971	Hawaii	627

Data source: Dr. William H. Bayliff, Inter-American Tropical Tuna Commission.

LARVAL SURVIVAL AND YEAR-CLASS STRENGTH

Rothschild (1965) conceded that environmental conditions a few months prior to the Hawaiian fishing season affect the availability of skipjack but felt that the large variability in catch rates is due to variability in the year-class strength. The variability in catch rates is also apparent within the two broad categories of years defined earlier in this paper. In the next section it will be shown, however, that the variability can be caused by variations in the current field. Nevertheless, year-class strength is not excluded as an additional cause for the variations in catch rates. It was previously noted that the large interyear differences in sea-air interaction processes observed during the TWZO investigation would affect productivity (plant production) and, hence, also larval survival. In mid- and high latitudes, winter overturn regularly replenishes the nutrients of the surface layer. In a large portion of the tropical and subtropical ocean this cyclical replenishment does not take place and a permanent pycnocline inhibits its vertical exchange of the surface nutrient-deficient with the deeper nutrient-rich water. Other than in areas of upwelling such as along the equator and possibly near islands, nutrients enter the surface layer by eddy diffusion. A net heat gain in the tropical and subtropical oceans tends to increase the stability of the pycnocline and thus inhibits the eddy diffusion process. Wind stirring, vertical current shear, and internal waves tend to enhance eddy diffusion. The wind speed also affects the evaporation which, in turn, affects the net heat exchange across the sea surface. The evaporation rate may be so large that there is a net heat loss from the sea surface and convective overturn takes place, increasing the nutrient supply of the surface layer.

Increased vertical diffusion across the pycnocline due to favorable sea-air interactions may have subtle effects in that it need not be reflected as an increase in nutrient concentration. In areas where nutrients limit productivity, an increase in the nutrient supply into the surface layer can be entirely exhausted by an increase in productivity. Thus, a low phosphate concentration and absence of a seasonal variation in the trade wind region of the North Pacific Ocean does not preclude variations in productivity.

The sea-air interactions in the trade wind zone from January to April 1964 (Table 4) favor a larger nutrient supply by diffusion and, therefore, higher productivity than do those for the same months of 1965. Consequently, a better supply of primary producers in 1964 should have enhanced larval survival. The TWZO larval captures in 1964 and 1965 are consistent with this proposition. There is presently no information to verify the hypothetical sequence of events.

In this discussion the results of the TWZO investigation are used to illustrate what probably takes place throughout the tropical and subtropical oceans and, therefore, in all the skipjack spawning areas. The illustration does not imply that the North Equatorial Current or the Hawaiian waters are major skipjack spawning grounds.

The sequence of events described is amenable to quantitative study. Productivity models exist, such as the one used by Parsons and Anderson (1970), that can be adapted to reflect the environmental changes of the skipjack spawning areas. An integral part of the productivity studies must be adequate sampling of the animal community, including skipjack larvae, that directly depend on the initial stages of the food chain. Those studies would lead to a recruitment or year-class strength model that complements the drift model. Development of a year-class strength model is not within the scope of this paper.

A DRIFT MODEL

The displacement of a fish school was expressed above by

$$S = S_W + S_F.$$

Here I wish to consider only the contribution to the total displacement of fish schools caused by the currents, S_W, in a portion of ocean between lat 10° and 25°N, and long 120° and 160°W, the model ocean. In this idealized, rectangular ocean the distances between degrees of latitude and

longitude are equal, and there is a geostrophic current and a wind-driven current. The increments of displacement of a fish school or a drifting object by currents are expressed by

$$\Delta S_W = V_W \Delta t = (V_G + V_E)\Delta t,$$

where V_W, the velocity of the water, is the sum of the geostrophic current, V_G, and the wind-driven current, V_E. V_G and V_E are functions of position and of time. Because the velocities are vectors, numerical integration (summation of increments) is facilitated by using zonal and meridional components of the displacement

$$\Delta X = (V_{GX} + V_{EX})\ \Delta t,$$

$$\Delta Y = (V_{GY} + V_{EY})\ \Delta t, \text{ respectively.}$$

The position of the fish school after n equal increments of time, Δt, is

$$X_n = X_0 + (V_{GX} + V_{EX})_1 \Delta t + (V_{GX} + V_{EX})_2 \Delta t + \ldots + (V_{GX} + V_{EX})_n \Delta t,$$

$$Y_n = Y_0 + (V_{GY} + V_{EY})_1 \Delta t + (V_{GY} + V_{EY})_2 \Delta t + \ldots + (V_{GY} + V_{EY})_n \Delta t$$

with an initial position X_0, Y_0.

In the model rectangle of ocean the meridional distribution of dynamic height varies sinusoidally according to

$$A_0 + C(t) \cos \frac{2\pi}{L(x)}(y-\alpha).$$

The minimum dynamic height is at lat 10°N and the maximum slopes northward from lat 20°30′N at long 160°W to lat 26°30′N at long 120°W (Figure 9). Thus, the geostrophic flow is zonal near lat 10°N but acquires a meridional component at higher latitudes. The amplitude of dynamic height, $C(t)$, in the sinusoidal distribution varies seasonally. The zonal component of the geostrophic current is expressed analytically by

$$V_{GX} = -K_i \left(\frac{2\pi}{L(x)}\ C(t)\ \sin \frac{2\pi}{L(x)}\ (y-\alpha) \right).$$

The seasonal variation of the amplitude,

$$C(t) = -[0.142 + 0.05 \cos 30(t + 1.13)],$$

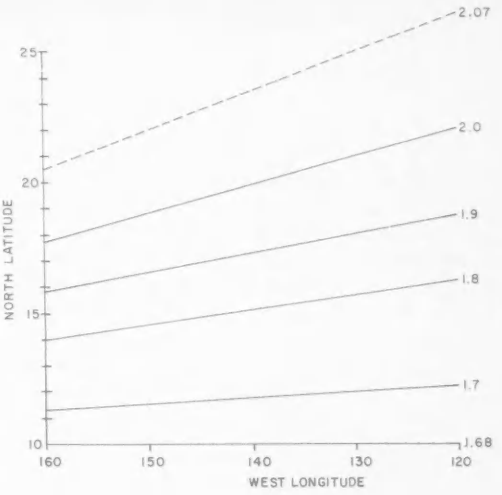

FIGURE 9.—Dynamic topography of model ocean (dynamic meters) at the time of maximum velocity.

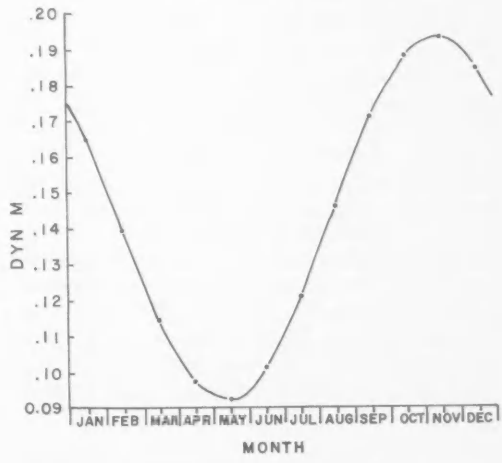

FIGURE 10.—Seasonal variation in amplitude, $C(t)$, for the harmonic expression of dynamic height as a function of latitude.

is shown in Figure 10.

The wave length, a function of longitude, x, is twice the width of the current: $L(x) = 69 - 0.3x$.

The meridional component of geostrophic current is given as a function of latitude, y, longitude, x, and the zonal component of geostrophic current, V_{GX}:

$$V_{GY} = -\frac{(y-10)}{230-x} V_{GX},$$

where x and y are the degrees of longitude and latitude in the model ocean, with the coordinates positive westward and northward. $L(x)$ is given in degrees latitude, and t is the time of the year in months. The phase angle, α, equals 10°, and in the dynamic height expression A_0 equals 1.875 dyn m. The zonal component of geostrophic flow in cm sec^{-1} is given by

$$K_1 = \frac{61.69}{\sin y}.$$

In the drift model it is most convenient to express the flow in nautical miles per month with

$$K_1 = \frac{862.9}{\sin y}.$$

The wind-driven current is based on the wind stress values of the Scripps Institution of Oceanography (University of California, 1948). The zonal and meridional components of stress were averaged between long 120° and 160°W for each month of the year and each latitude band 10°-14°N, 15°-19°N, and 20°-24°N. The variation with time, t, of the zonal components, τ_x, and the meridional components, τ_y, of the wind stress are adequately defined by the harmonic functions in Table 6, and shown in Figure 11.

The meridional and zonal components of Ekman transport are calculated from the equations $E_y = -\tau_x/f$, and $E_x = \tau_y/f$, where f is the Coriolis parameter. Most of the transport takes place in the upper 100 m of ocean. Here, it is assumed that all the transport takes place in the upper 100 m. $V_{EX} = -K_2 \tau_y$ and $V_{EY} = K_2\tau_x$ then give the mean wind-driven current for this depth in cm sec^{-1} if K_2 for latitude bands 10°-14°N, 15°-19°N, and 20°-24°N is 3.17, 2.29, and 1.79, respectively. Again, for application in the drift model it is most convenient to express the drift current in nautical miles per month, and K_2 for latitude bands 10°-14°N, 15°-19°N, and 20°-24°N becomes 37.5, 27.0, and 21.3.

TABLE 6.—Harmonic functions of the zonal component, τ_x, and meridional component, τ_y, of wind stress in dynes cm^{-2}. The time of year, t, is in months.

lat 10°-14°N,	$\tau_x = 0.91 + 0.544 \cos 30\ (t-2.1)$
lat 15°-19°N,	$\tau_x = 0.8 + 0.188 \cos 30\ (t-1.2)$
lat 20°-24°N,	$\tau_x = 0.56 + 0.022 \cos 30\ (t+1.2)$
lat 10°-14°N,	$\tau_y = 0.56 - 0.330 \cos 30\ (t-2.5)$
lat 15°-19°N,	$\tau_y = 0.47 - 0.04 \cos 30\ (t-0.2)$
lat 20°-24°N,	$\tau_y = 0.34 + 0.045 \cos 30\ (t-1.4)$

Using the geostrophic and wind-driven current speeds, the drift displacements can be calculated. Once per month 11 objects are introduced along the eastern boundary of the model ocean, equally spaced from lat 10° to 20°N. Displacements are calculated and the new position at the end of the month is determined. Again, displacements are calculated for the new time and position, and the positions at the end of the second month determined. These calculations are repeated for 36 months or stopped before that time if the western boundary (long 160°W) is crossed or when the object drifts into easterly (negative) flow at the northern boundary of the westerly setting geostrophic current. It is assumed that the drifting objects move up and down in the upper 100 m much as a skipjack school may be doing.

The result of the numerical integration is shown in Figure 12. The location of drifting objects that were introduced at the beginning of April, May, and June at lat 10° to 20°N along long 120°W are traced across the model ocean in steps of 3 months. After 12 months all drifting objects are north of lat 15°N. The objects that began north of lat 15°N are the first to drift into the northern, slow portion of the Equatorial Current and are overtaken by the objects that began at and to the south of lat 15°N. Thus a meridional distribution of objects at the beginning becomes oriented along the northern edge of the model equatorial current after 24 months of drifting.

Another presentation of the results (Figure 13) shows the location, after 30 months, of all objects that were introduced at the beginning of each of the 30 months along long 120°W. The most westerly position reached by objects during each quarter is indicated by a dotted line. Again, it is evident that objects initially located south

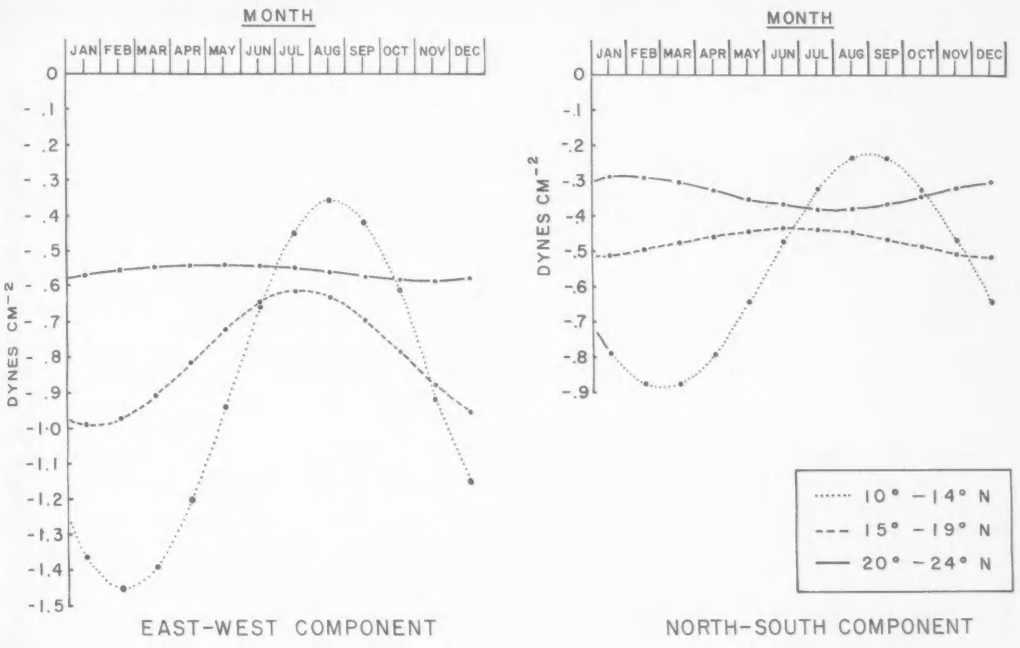

FIGURE 11.—Zonal and meridional components of wind stress in latitude bands 10°-14°N, 15°-19°N, 20°-24°N averaged between long 120° and 160°W (University of California, 1948). Stress is positive if directed to the east and north, respectively.

of lat 15°N rapidly drift northward. Objects appear to concentrate on the southern and northern edge of their distribution and then merge west of long 150°W in a relatively narrow band between lat 18° and 22°N. Lost in the presentation are a few objects that drifted across the northern edge of the equatorial current in the western portion of the model ocean and those that drifted west beyond long 160°W. In the western part of the model area considerable mingling of objects introduced in different seasons takes place. In some 1-degree units of area are found objects that were introduced during 3 seasons.

The concentration of drifting objects at the southern edge of their distribution is caused by the seasonal difference in the convergence of the meridional wind-driven current. The zonal component of the trades is stronger from November to June at lat 10° to 14°N then at lat 15° to 19°N but weaker from June to November (Figure 11). Consequently, the meridional component of wind-driven current is strongly convergent from November to June but weakly convergent or divergent during the remainder of the year. The effect of this seasonal difference is illustrated in Figure 14. Note that in the first case with a high meridional wind-driven current only 4 objects are left south of lat 15°N but 11 objects are left in the second case. Again, in the first case with strong meridional convergence there were 14 objects between lat 15° and 17° but 8 objects for the second case.

The seasonal variation of meridional wind-driven current inferred from the lat 15° to 19° and 20° to 24°N curves in Figure 11 is smaller than it is south of lat 15°N. Consequently the northward drift near lat 20°N is not as large as in the example given above. Near this latitude, however, the southward component of the

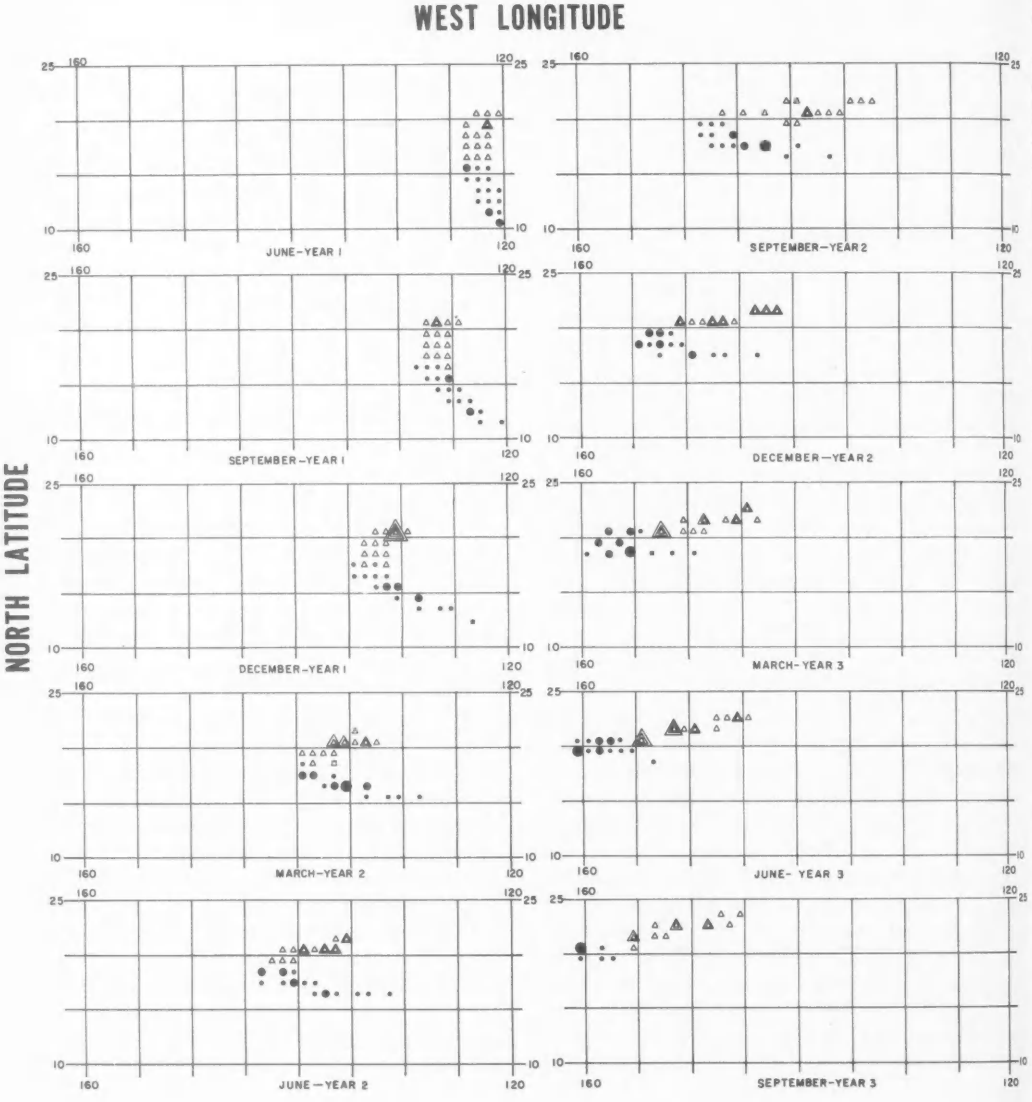

FIGURE 12.—Location of drifting objects every 3 months after being introduced during April, May, and June of the first model year at long 120°W. Triangles denote objects introduced north of lat 15°N. The number of drifting objects, if there are more than one per 1-degree square, is indicated by concentric triangles or circles.

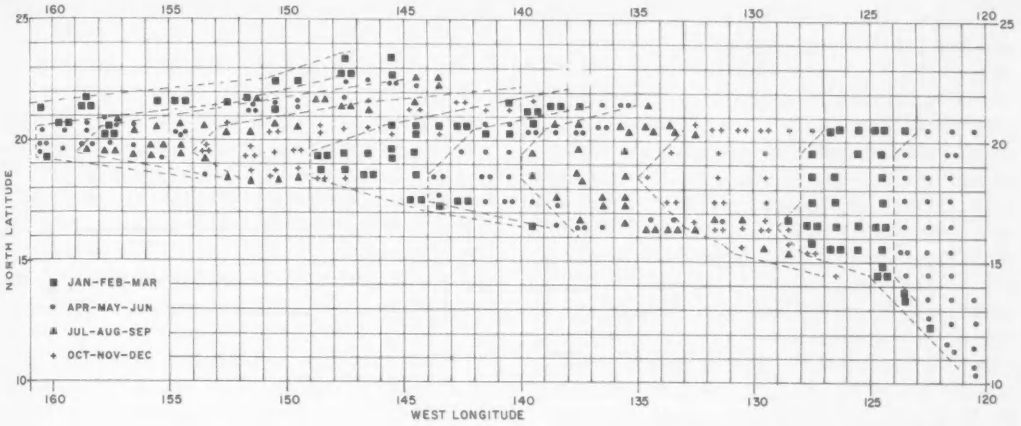

FIGURE 13.—Locations of drifting objects in June of the third model year that were introduced in each of the previous 30 months at long 120°W. Dashed lines indicate most westerly location reached by objects introduced every quarter.

geostrophic current (Figure 9) becomes important. The effect of convergence of this component of flow with the northward wind-driven current is evident at the northern edge of the distribution of drifting objects in Figure 13.

As the objects drift westward north of lat 18°N and west of long 140°N, they enter the region of decreasing speed in the North Equatorial Current (Figure 9) and therefore tend to accumulate further (Figure 13).

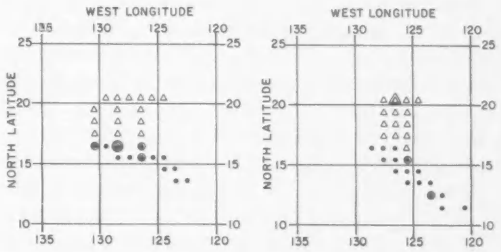

FIGURE 14.—Left Panel: Position of objects in March that were introduced at long 120°W during the previous October, November, and December. Right panel: Positions of objects in September that were introduced at long 120°W during the previous April, May, and June.

THE MODEL OCEAN AND SKIPJACK

The minimum duration of drift of objects from long 120°W to the quadrant north of lat 19°N and west of long 155°W ranges from 21 to 23 months (Table 7). These times are of the same order of magnitude as the times skipjack tagged in the eastern Pacific were free except for the two skipjack tagged near Clipperton Island (Table 5). If the model ocean is realistic, these results indicate that the mean velocity of the fish relative to the water (V_F) is small compared to the mean velocity of the water (V_W). The paths of the fish, of course, are not known and many routes and modes of travel behavior can be postulated. However, there is one, the simplest mode

TABLE 7.—Minimum duration of drift from long 120°W to the quadrant north of lat 19°N and west of long 155°W.

Month of start	Year and month of arrival		Duration of drift in months
Jan.	2d	Oct	22
Feb.	2d	Nov	22
Mar.	2d	Dec	22
Apr.	3d	Jan	22
May	3d	Jan	21
June	3d	Feb	21
July	3d	Mar	21
Aug.	3d	Apr	21
Sept.	3d	Jun	22
Oct.	3d	Aug	23
Nov.	3d	Sep	23
Dec.	3d	Oct	23

of travel, that must be considered—namely, randomly swimming skipjack drift westward in the North Equatorial Current. This mode of travel means that skipjack entering the North Equatorial Current in the eastern Pacific do not migrate in the sense that they are actively swimming towards a destination. These skipjack are concentrated, or converge with the trade wind-driven water near lat 15°N, and near lat 20°N they are concentrated by the southward component of the geostrophic current and the northward component of wind-driven current. As the fish schools approach Hawaii, they further accumulate because of decreasing geostrophic flow.

COMPARISON OF THE MODEL WITH THE REAL OCEAN

In the model the effects of characteristic features in the geostrophic and wind-driven currents on the distribution of drifting objects were demonstrated. The simplest analytic expressions for the North Equatorial Current and the wind distribution were used in order to facilitate numerical integration. How well do these simple expressions reflect the average conditions as we know them to exist in the ocean?

First, consider the field of geostrophic flow. In the model area, data from historic oceanographic cruises are sparse, but a chart of the Pacific Ocean dynamic topography prepared by Reid (1962) shows that maximum and minimum dynamic heights differ by about 0.4 dyn m as they do in Figure 9. Average geostrophic speeds in the model and the ocean are therefore of the same magnitude.

There is some uncertainty in the width of the North Equatorial Current at long 120°W. At this meridian Reid's chart shows the northern edge to be at about lat 15°N. A qualitative geostrophic interpretation of Barkley's (1968) depth of the sigma-t 25.4 surface, in the main pycnocline, places the northern edge near lat 25°N at long 120°W and near lat 21°N at long 160°W.

Many more bathythermograph data than oceanographic station data are available. A geostrophic interpretation of Wyrtki's (1964) depths of the center of the permanent thermocline places the northern edge of the Equatorial Current to the north of lat 20°N in the eastern part of the model area. More recently, charts of the temperature distribution at 400 ft prepared from bathythermograph data by Robinson and Bauer[8] places the northern edge of the Equatorial Current near lat 18° or 19°N at long 160°W and from about lat 20° to 25°N at long 120°W. In the vicinity of the Hawaiian Islands, the northern edge of the Equatorial Current inferred from Robinson's charts compares well with the results of the TWZO investigation (Charnell, Au, and Seckel, 1967a,b,c,d,e,f).

The seasonal variation of the geostrophic flow in the North Equatorial Current observed during the TWZO investigation was reported by Seckel (1970c). The meridional slope of dynamic height between lat 10° and 20°N computed for each cruise of this investigation, reflecting the mean, zonal component of geostrophic current

[8] Robinson, M. K., and R. A. Bauer, Atlas of monthly mean sea surface and subsurface temperature and depth of the top of the thermocline, North Pacific Ocean. Unpublished manuscript reproduced by Fleet Numerical Weather Central, 1971.

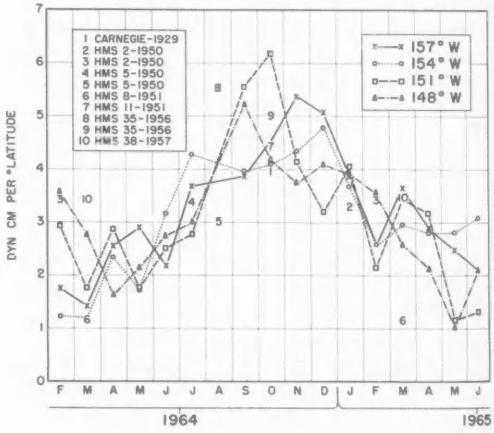

FIGURE 15.—Meridional slopes of dynamic height, lat 10° to 20°N for every month from February 1964 to June 1965 of the Trade Wind Zone Oceanography cruises, connected by straight lines. Numerals indicate the meridional slopes of dynamic height for the cruises of the *Carnegie*, 1929, and *Hugh M. Smith* (HMS), 1950-1957.

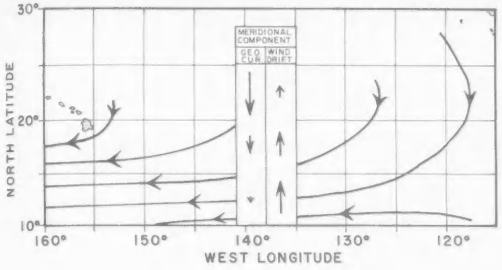

FIGURE 16.—Schematic presentation of geostrophic flow in the North Equatorial Current with meridional components of geostrophic flow and wind-driven current (insert).

is shown in Figure 15. Also shown are the meridional slopes computed from historic cruises. These values fall into the seasonal pattern. Qualitative interpretations of Wyrtki's and Robinson's charts referred to above confirm the TWZO results and show that the seasonal variation extends to long 120°W.

The model east-west component of geostrophic flow, therefore, compares well with available oceanographic station and bathythermograph data. Although a small north-south component of geostrophic flow is computed from the analytical expression of dynamic height used in the model, this component is not adequately represented. A schematic presentation of geostrophic flow in Figure 16 illustrates that south of lat 15°N the Equatorial Current is essentially zonal but north of this latitude, the meridional component increases to north of lat 20°N where the geostrophic current is mostly meridional.

The underestimate of the meridional component of geostrophic flow in the northern portion of the model has the effect of shifting the main concentration of drifting objects north. The underestimate, however, does not affect the duration of east to west drift.

In the model only drift within the North Equatorial Current is considered and objects that pass across its northern boundary are not plotted in Figures 12 and 13. In the ocean, drifting objects that pass across the northern boundary are carried back into the convergence by easterly and southerly components of geostrophic flow. Thus, the concentration of drifting objects in the convergence near Hawaii is expected to be larger than shown in the model.

The wind stress values of the Scripps Institution of Oceanography (University of California, 1948) that were used represent average conditions in the trade wind region. Important in the drift model is a northward component of wind drift that is proportional to the zonal component of wind stress. This characteristic feature is not lost by averaging wind stress values in 5-degree latitude bands between long 120° and 160°W.

The simple procedure of dividing the Ekman transport by 100 m to obtain the wind-driven current may be questioned. This procedure, however, affects the magnitude of wind drift and not the characteristic feature essential in the drift model; a meridional component of wind-driven current.

The results of the drift model are therefore the same as those to be expected in the portion of ocean under consideration if average conditions prevail. Drifting objects or skipjack schools uniformly distributed along long 120°W between lat 10° and 20°N drift westward and southward with the geostrophic North Equatorial Current. A component of surface wind-driven current in the direction to the right of the wind stress vector displaces the skipjack schools northward. In consequence of the converging flow fields, the concentration of drifting schools increases westward much as in the model.

The drift model is based on a smooth North Equatorial Current representing average conditions. From Figure 17, showing the time variation of the east-west component of geostrophic flow at long 148°W during the TWZO investigation, it is evident that the North Equatorial Current is not a smooth flowing stream. Cells of high westerly speeds alternate with low speeds or even easterly flow directions. A fish school caught in high westerly flow of more than 25 cm sec^{-1}, such as occurred near lat 15°N during August to October 1964, would in 2 months be carried about 1,300 km (700 nautical miles) westward. Thus, much shorter drift durations can occur than those given in the model. An

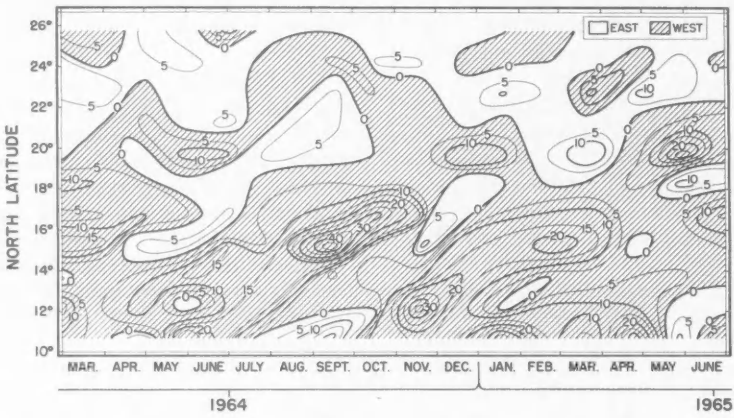

FIGURE 17.—Zonal component of geostrophic flow (cm sec^{-1}) at long 148°W from Trade Wind Oceanography cruises, March 1964 to June 1965. Hatching indicates flow to the west.

example are the skipjack that were tagged near Clipperton Island (Table 5).

Large interyear differences in mean geostrophic flow take place. Between March of 1964 and 1965, the average geostrophic speeds, as interpreted from the meridional slopes of dynamic height, Figure 15, differed by more than a factor of two. In August, historic cruise data indicate a factor of 1.8 in the interyear difference. Large interyear differences in wind stresses as listed in Table 4 also occur (Seckel, 1970b). The path of a drifting skipjack school therefore is expected to vary from year to year. Also to be expected are year-to-year changes in location and intensity of the converging southward component of geostrophic flow with the northward component of wind drift, as evidenced in Figure 4.

SUMMARY AND DISCUSSION

Oceanographic studies have led to the discovery of environmental changes that are associated with the seasonal and interyear differences in availability of skipjack to the Hawaiian fishery. Important is the seasonal northward movement in spring and summer of low salinity, California Current Extension water that replaces high salinity, North Pacific Central water in the Hawaiian region. Intrusion of the California Current Extension water coincides with the seasonal increase of skipjack landings. Koko Head salinities as well as the larval distributions observed during the TWZO investigation indicate that the high salinity range (34.6 to 34.8‰) of the California Current Extension is most favorable. Failure of this water to move into the fishing region results in low catches.

Northward movement of surface water during late winter and early spring causes warm advection or a warming of the water earlier than can be expected from heat exchange across the sea surface. If initial warming occurs before the end of February catches tend to be good. Initial warming in March indicates unfavorable conditions.

Using as indices the time of initial warming and the spring and summer salinity in the Hawaiian Islands, one finds that catches are normal when either or both indices are unfavorable, and exceptional when both indices are favorable. Normal annual catches average 3,600 tons and range from 2,700 to 4,400 tons. Exceptional annual catches average 5,800 tons and range from 4,940 to 7,330 tons.

Both indices reflect dynamic conditions in the environment. This view is supported by results of the TWZO investigation. A diffuse salinity

gradient separating the North Pacific Central water from the California Current Extension water in 1964 (Figure 4) coincided with a normal fishing year, a sharp gradient in 1965 coincided with an exceptional year. The character of the gradient is determined by the currents.

The importance of currents in marine biology is recognized. Examples of how currents affect marine life have been given by Laevastu and Hela (1970). However, the active part that ocean currents play in the migration of adult fish has not been stressed. The role of currents in fish migrations including the movements of fish without reference to landmarks has been described by Harden Jones (1968). The role has been covered only qualitatively, however, and tuna migrations were not amongst his examples.

The destination and migration path of a fish is the vector sum of the water velocity and the swimming velocity relative to the water. The contribution of the currents to the migration of skipjack that enter the North Equatorial Current in the eastern Pacific has been examined by means of a simple drift model. Essential in this model are the geostrophic flow of the North Equatorial Current and a northward component of surface wind-driven current resulting from the trades. In this current system floating objects or fish schools uniformly distributed between lat 10° and 20°N at long 120°W would be concentrated by the meridional component of wind-driven flow as they drift westward.

This concentrating mechanism is evident in Figure 13 where the southern boundary of the drifting objects (fish schools) shifts northward with increasing west longitude. Additionally, objects (fish schools) are concentrated where a southerly component of geostrophic flow and a northerly component of wind drift converge north of lat 20°N (Figure 13). The minimum time required to reach the Hawaiian Islands ranges from 21 to 23 months (Table 7). The computed drift time is of the same magnitude as the time of freedom of tagged fish (Table 5).

Before examining the consequences of this result, it is useful to place some limits on the navigational abilities of skipjack. (See also Harden Jones, 1968.) In terms of physics, it is hard to understand how, in the open ocean without a fixed reference, a fish knows that he is in a current. Only in accelerating flow would he be able to feel a force. The fish, therefore, does not know whether he is swimming with or against the current.

Easier to understand is the ability of a fish to swim in the direction of his choice. He may also know from the water properties, the type of forage, or from celestial navigation, that he is not in the area of his choice and therefore may set a course for a more desirable environment. Even in this eventuality, his destination is affected by the current.

Thus, the distribution of skipjack, whether they swim randomly and drift with the current or swim in a predetermined direction, is affected by the northward component of the wind-driven current and the convergence near the northern edge of the Equatorial Current.

As a result of the numerical model it can be postulated that a possible, and the simplest, mode by which skipjack travel from the eastern Pacific to Hawaii, is by swimming randomly and drifting with the current. This mode of travel is consistent with the empirical associations that were described and does not contradict the applicable portion of Rothschild's (1965) migration model. Rothschild statistically related the time of warming in Hawaiian waters with annual landings and stated " . . . that 44 percent of the variation in catch is accounted for by time of warming, the other 56 percent being unexplained." This statement can be misinterpreted in that it implies a causal relation between time of warming and catch rates. Rothschild apparently wishes to demonstrate that there is a variation in catch rates that is not associated with the variation of time of warming. This conclusion is also evident from Figure 2 which shows a relatively large range of catch rates within the exceptional and normal types of years. Rothschild examined the differences and their causes in the size frequency distributions of the eastern North Pacific and Hawaiian skipjack fisheries. He concluded " . . . that year-class associated phenomena play an important role in controlling the abundance of skipjack in Hawaiian waters." Rothschild, however, neglected to consider the effects of currents on the distribution of skipjack.

Currents, as is evident from the drift model results, also cause variability in annual landings and in the size-frequency distributions. It was noted that in the western portion of the model, drifting objects were found in a single degree-square area that had been introduced along long 120°W during 3 seasons. If the drifting objects are fish schools an age difference of 9 months would be reflected in the sizes of fish caught.

TWZO results have shown that the mean geostrophic flow in the North Equatorial Current can vary by up to a factor of 2 from year to year and that there are large interyear differences in the wind stress. The time of drift from the eastern to the central North Pacific can therefore vary more than the range indicated by the drift model, and it is possible for skipjack schools that entered the North Equatorial Current during 1 year to catch up with those that entered during the previous year.

Rothschild (1965) also states that lack of growth, or slow growth, as reflected by size frequency distributions, can be due to a movement of fish through the fishery. This movement can be fish schools drifting with the currents.

The size of fish caught in the Hawaiian fishery is also affected by the time, place, and size of fish entering the North Equatorial Current. Fish recovered in Hawaii were tagged in April, June, September, October, and November near Baja California, the Revillagigedo Islands, Clipperton Island, and near the boundary of the Equatorial Counter Current and South Equatorial Current at lat 4°N, long 119°W (Table 5). The size-frequency distributions of skipjack caught in the Baja California and Revillagigedo Islands regions presented by Rothschild showed large variation from season to season and year to year. Williams (1972), in another article of this issue, proposes three alternate migration models that explain the recruitment of skipjack into the eastern North Pacific. He concludes that oceanographic conditions in the central and eastern Pacific have a vital controlling effect on the abundance of skipjack in the eastern Pacific fishery.

Finally, year-class strength determined by survival of larvae and juveniles, as suggested by Rothschild, is not ruled out as contributing to the catch rate variations in the Hawaiian fishery. Large interyear differences in oceanographic conditions as reflected by the sea-surface temperatures at Christmas Island (Seckel and Yong, 1971) and the large interyear differences in sea-air interactions observed during the TWZO investigation undoubtedly affect the survival of larvae, as suggested previously, and, therefore, the population size. However, variations of year-class strength of medium and large fish in the Hawaiian fishery may be masked by the effects of varying currents in the eastern and central North Pacific on the distribution of skipjack.

An attractive aspect of the drift hypothesis is its simplicity. Skipjack while in the North Equatorial Current need not do, know, or remember anything other than to search for food. They need not be able to recognize the concentration of salt in the water or distinguish between water types and then know what corrections to make in order to reach the preferred location. They need not be able to recognize time of warming early in the year and then know whether they should or should not enter the Hawaiian fishery. The salinity and temperature indices correlate with availability of skipjack in Hawaiian waters, because the same water motions that affect the distribution of temperature and salinity in the North Equatorial Current (Seckel, 1962) also affect the distribution of skipjack.

In general, it is important to recognize that what is loosely called migration consists of the two components of travel: one resulting from the mean velocity of the water (V_W) and the other from the mean velocity of the fish or fish school relative to the water (V_F). Extreme situations are those where one component is very much smaller than the other so that it can be neglected. There are probably many cases where V_F and V_W are of the same magnitude. An example of these are the migrations of Pacific salmon (Royce, Smith, and Hartt, 1968). During certain times of the oceanic life of salmon, average travel speeds ($V_F + V_W$) of about 6 to 12 miles per day (13 to 26 cm sec^{-1}) are indicated. Ocean currents (V_W) with speeds of only 5 to 10 cm sec^{-1} are therefore of the same mag-

nitude as the mean velocity of the salmon relative to the currents and cannot be neglected. In fact, it is important to consider V_F rather than (V_W + V_F) when studying the navigational abilities or behavior of fish. Even if V_W is one order of magnitude smaller than V_F, when travel times of 1 or 2 years are involved, V_W may not be neglected and the destination will reflect the effect of the current system.

An example of V_W being negligible in comparison with V_F is the travel of albacore across major portions of the North Pacific Ocean. The example where V_F is very much smaller than V_W may be the travel of skipjack from the eastern to the central North Pacific Ocean.

When skipjack reach the vicinity of islands a fixed reference becomes available and the swimming behavior is likely to become different from that in the open ocean. The fish that were tagged by a sonic device near the Hawaiian Islands (Yuen, 1970) are an example of such behavior. The current field is also affected by the proximity of islands. Although the relative magnitudes of the current velocities and swimming velocities may differ from the open ocean case, both velocities must still be considered. The travel behavior of skipjack near islands is, however, a different problem from that considered in this paper because the time scale is in the order of hours rather than weeks.

Finally, the relative magnitude of V_F as compared with V_W may vary throughout the travel history of a particular species of fish. This variation was documented by Royce et al. (1968) for the case of Pacific salmon and may also apply to albacore. Williams (1972) tends to favor "active" migration of skipjack into the eastern North Pacific fishery. Therefore, V_F may not be small when compared with V_W throughout the travel history of skipjack.

CONCLUSION

A plea is made in this paper by way of proposing a model, much as was done by Rothschild (1965), to progress from the exploratory phase of skipjack distribution studies to the experimental phase. Results from exploration (assemblage of data collected without experimental design) were used to demonstrate empirical associations between the availability of skipjack to the Hawaiian fishery and environmental indices. Important to an understanding of the life history is the linkage between environment and the distribution of skipjack that the empirical associations do not provide.

Insight into the linkage mechanisms is gained if the associations are used as leads to hypotheses or models that can be tested experimentally.

Modern technology together with the powerful analytical tools now available make it possible to construct a complete migration-distribution model of skipjack from the eastern and central North Pacific Ocean. In such a model the North Equatorial Current portion would be linked with one of the eastern Pacific models of Williams (1972) and with a larval survival-year class strength model. Swimming velocities of skipjack can be simulated and included in the model. Numerical evaluation of such a model depends upon adequate environmental information, e.g., large-scale sea-air interaction processes, geostrophic and wind-driven velocities of ocean currents.

Important elements that were not discussed in this paper must be evaluated. For example, there are the effects of dispersion on the distribution due to the random motions of skipjack schools and due to large eddies within the current system. Currents, either geostrophic or wind driven, are not necessarily constant within the range of vertical movement of skipjack. The current drift must therefore be tuned to the depth range within which skipjack swim.

The sources for the required environmental information are meteorological observations from ships, that in the future may be supplemented by buoys. Geostrophic current speeds can be monitored by the use of vertical temperature sections obtained from merchant ships regularly traveling specific routes. The dispersive effect of random fish school motions can be determined by using a sonic tag to track skipjack as was described by Yuen (1970). The dispersive effect of eddying currents can be determined from drifting buoys whose positions are monitored by satellite. Predicted drift or progress

of fish schools based on numerical integration can be verified by drifting buoys and by following fish tagged with a sonic device.

The experimental approach will also aid to answer such questions as the following: Why is there little evidence of spawning between the eastern North Pacific and long 140°W? Why are skipjack schools not evident at the sea surface? Is the productivity of the water adequate to support the skipjack schools with a slow net movement? What is the effect of varying forage abundance on the search pattern and therefore the dispersion of skipjack schools?

The implications of an experimental, numerical approach to the skipjack distribution problem are far-reaching. The principal results of the simple drift model used in this paper will hold in a more sophisticated model where observed rather than climatic boundary conditions are used. The results indicate that the probable drift path and concentration of skipjack schools is predictable. Such predictions will increase the harvest efficiency of the skipjack resource. The insight gained into the life history of skipjack, particularly if the survival mechanisms of early life stages are included in the model, will permit elegant management of the skipjack resource.

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SAMPLING ANCHOVY LARVAE WITH A PLANKTON PURSE SEINE[1]

GARTH I. MURPHY[2] AND ROBERT I. CLUTTER[3]

ABSTRACT

A miniature purse seine (100 ft by 21 ft) was constructed of 333 μ Nitex. It was used in Kaneohe Bay, Hawaii, together with a 1-m plankton net constructed of the same material in order to evaluate the sampling efficiency of the towed plankton net on anchovy larvae (*Stolephorus purpureus*). The results show that during the day, the purse seine is at least an order of magnitude more efficient for larvae over 5.5 mm in length. The largest larva caught by the plankton net was 14.5 mm and by the purse seine 29.5 mm. At night the plankton net was relatively more effective than during the day, catching about 60% as many larvae as the purse seine over the interval 3.5-19.5 mm. The maximum size taken increased to 21.5 mm, but the maximum taken by the purse seine increased to 50 mm. An attempt was made to rationalize the difference between the day plankton net and purse seine catches by a geometric model involving alarm distance and larval swimming speed. The results are moderately satisfactory.

More limited data on anchovy larvae catches by a 10-ft Isaacs-Kidd trawl, ¼-m, ½-m, and 1-m plankton nets are presented and discussed in the framework of the meter net-purse seine data. These analyses suggest one or more paradoxes in the larval escape problem, or that the data are inadequate.

The classical approach to sampling zooplankton is the towed net. This has two disadvantages: an unknown fraction of the organisms in the path of the net escape by dodging and the net integrates the organisms living along a transect of considerable length—making it difficult to consider the catch from a tow as representing an assemblage of coexisting organisms. The dodging problem has been considered by (among others) Fleminger and Clutter (1965) with respect to planktonic crustacea, Ahlstrom (1954) and Isaacs (1965) with respect to fish larvae, and McGowan and Fraundorf (1966) with respect to zooplankton. A general review of the problem is given in UNESCO (1968).

In recent years there have been attempts to apply community theory to the pelagic realms, e.g., Fager and McGowan (1963) and Venrick (1971). Such attempts should involve samples that represent organisms likely to be coexisting. Grab sampling such as used by Venrick (1971) for diatoms is the obvious method of choice as the scale of coexistence can be specified with precision, but existing grab samplers engulf so little water that they are not likely to afford meaningful information on the medium and large zooplankton. The probability that a towed net will integrate several communities has also been recognized and several solutions developed with respect to subdividing a tow, e.g., Longhurst et al. (1966). But if the tow is subdivided small enough for the dimensions to be meaningful, it will not likely strain enough water to sample the less abundant forms.

The purse seine (and other nets of similar design) is an extremely effective large volume grab sampler in wide use by commercial fishermen. Essentially, a wall of net is set in a circle and the bottom closed (pursed) by drawing on the purse lines. This kind of grab sampler can only be effective at the surface and, therefore, is of general application only in shallow water or under circumstances where the surface fauna is of interest.

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The primary purpose of the present study is to evaluate the extent that a large grab sampler (miniature purse seine) can generate samples of fish larvae that are less biased than towed nets with respect to avoidance. The catches of an anchovy larva (*Stolephorus purpureus*) were enumerated from the samples. These were thought to be the most informative of the organisms captured by the net in part because they were present consistently in the samples, in part because they provide a spectrum of small to large zooplankton essentially constant in body form, and in part because there is a wealth of literature on the sampling of fish larvae, in particular, anchovy larvae.

DESIGN AND OPERATION OF THE NET

The net employed was patterned exactly, insofar as operational considerations are concerned, after that described in Hunter, Aasted, and Mitchell (1966), excepting that the body of the net was constructed of 333 μ Nitex.[4] The length of the Nitex section was 100 ft and the depth 21 ft. A small cod end was placed near the bitter end of the net.

The net was usually set in the form of an incomplete circle from a platform mounted on a 16-ft Boston Whaler, so that the net set off the port side. Closure of the circle was effected during the first stages of hauling. The operation from starting the set to pursing generally took less than 5 min. Hauling up the net required 15 to 20 min with two men at work. Figure 1 shows the net in the water at the start of pursing.

All of the data considered in this report were taken in Kaneohe Bay, Oahu, where swell is negligible and seas are generally less than 1 ft. It was tested in open ocean swell and in seas up to 4 ft. The operation was not affected by swell and seemed to be effective in seas of short period waves, although the effect of waves splashing over the float line of the net was not evaluated.

[4] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

One operational problem that we anticipated never materialized. We had feared that significant amounts of zooplankton would catch on the net as it was being hauled up. This did not happen even in the instance of chaetognaths, apparently because the plankton, being alive, avoided the mesh. During the final stages, it was necessary to carefully wash the catch toward, and finally into, the cod end.

FIELD AND LABORATORY METHODS

The primary objective of the study, comparison of the catches by the purse seine with catches by a meter net, dictated the field sampling pattern. Two skiffs were employed, one with the seine and the other with the meter net. As soon as the seine was set, the second skiff began towing the meter net as close to the seine as possible. The meter net was raised and lowered so as to proportionally sample the same water column fished by the seine. The plankton net was fitted with a Rigosha flow meter. Tows were generally 10 min in duration, but sometimes they were reduced to 5 min when clogging was a problem.

In the laboratory the total wet volume of the samples was measured. The entire sample was scanned for fish larger than 10 mm. Then either the entire sample or an appropriate aliquot was examined in detail, enumerating and measuring all anchovy larvae (*Stolephorus purpureus*), and enumerating anchovy eggs. The entire sample was then reconstructed by appropriate linear adjustments. Finally, all results were adjusted to numbers per 300 m^3. This value was selected because it was intermediate between the actual typical volumes of water strained by the two samplers, giving the advantage that the numbers to be dealt with are roughly the same as the actual numbers of organisms captured.

In all, there were 44 day stations and 10 night stations from Kaneohe Bay. The exact locations of the stations are not relevant to this study and so are not given. Most were made at Tester's stations 1, 2, 5, and 10 (Tester, 1951). Samples were roughly evenly spaced from November 29, 1966, to August 25, 1967.

FIGURE 1.—Underwater view of the plankton purse seine just as pursing was initiated. Photograph by Robert R. Harvey.

CALIBRATION OF SEINE

Although, as will be seen later, it is not absolutely necessary for some analyses to know exactly how much water was sampled by the seine, it is desirable to have a reasonably accurate estimate. The size of the net and idealized geometry of a perfect set suggest the net could surround about 500 m^3 of water.

Actual sets are not perfect, and an attempt was made to standardize for obvious imperfections by noting visually estimated percent efficiency during each set. These ranged from 60 to 100% with six from 60 to 65%, nine from 80 to 85%, and the balance (40) from 90 to 100%. All numerical data generated by the samples were adjusted to 100% efficiency.

Since metered plankton net samples were available from presumably the same water as the purse seine, it should have been possible, ideally, to calibrate each set by comparing the catches of some nonmotile component of the plankton, e.g., fish eggs. This was not possible because such items were not consistently present and, more importantly, because high amplitude, short-period patchiness was obviously generating high variability, even between such closely spaced samples.

The final decision was to use total sample volume as a measure of the water strained by the seine, i.e., the volume of water strained by the seine was estimated by comparing the total volume of wet plankton with the total volume of wet plankton taken by the metered plankton net. This was based on the hindsight fact that the volume of non-escapers, e.g., ctenophores, was very large compared with the volume of escapers, e.g., fish larvae, and therefore, the total volume was essentially independent of escapers. Several analytical techniques, e.g., regression, were considered and applied. These yielded estimates of the purse seine volume at 100% efficiency from 305 m^3 to 441 m^3. Finally adopted was a simple comparison of the geometric means (because the volumes were logarithmically distributed) of the two series after raising the meter net catches to 300 m^3 of water strained, and the purse seine catches to 100% efficiency. This yielded a value of 356 m^3 of water strained for the purse seine at 100% efficiency. The procedure was: geometric mean of 54 purse seine catches divided by the geometric mean of 54 300-m^3 plankton net catches multiplied by 300 equals mean purse seine volume of 356. This value, of course, remains an approximation. Any error has no effect on the analytical portions of this paper as the slopes of the length frequency curves are of primary concern. As indicated earlier, the primary purpose of the adjustments is to deal with reasonably real world numbers.

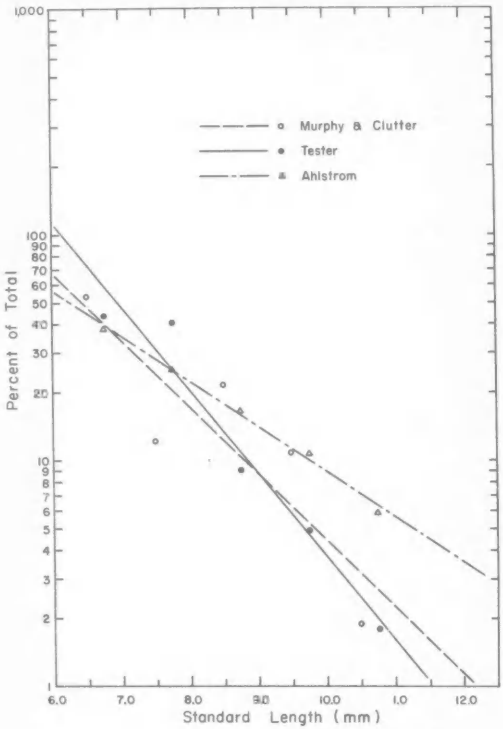

FIGURE 2.—Anchovy larvae catches reported by Ahlstrom (1965) on *Engraulis*, Tester (1951) on *Stolephorus*, and Murphy and Clutter (present paper) on *Stolephorus*. The lines are least square regressions.

RESULTS

DAY SAMPLES

As indicated earlier, the bulk of the sampling was done in the daytime. We used a meter plankton net as our measure of normal sampling efficiency. Because of this, it is of considerable interest to establish how the sampling efficiency of our meter net system compared with the experience of other investigators using the same equipment and towing speeds. This was done by comparing the slopes of our anchovy size-frequency curve with the results of an earlier study in Kaneohe Bay (Tester, 1951) and with the results of a massive program in the eastern Pacific on the northern anchovy (*Engraulis mordax*) (Ahlstrom, 1965).

The results of the three programs (Figure 2) are remarkably similar, and although the *Engraulis* data have a somewhat flatter slope, the difference is not significant, at least for the present purpose. This was not entirely unexpected since the eggs and larvae of *Stolephorus* are almost identical in size and appearance to those of *Engraulis*. We assume that our comparison of purse seine and plankton net catches of anchovy larvae is applicable to all anchovy larvae.

Our day purse seine and meter net data are compared in Figure 3 and Table 1. They indicate remarkable undersampling by the meter net. The break in the slope at 20 mm in the purse seine curve coincides approximately with the transformation from larva to juvenile. This may

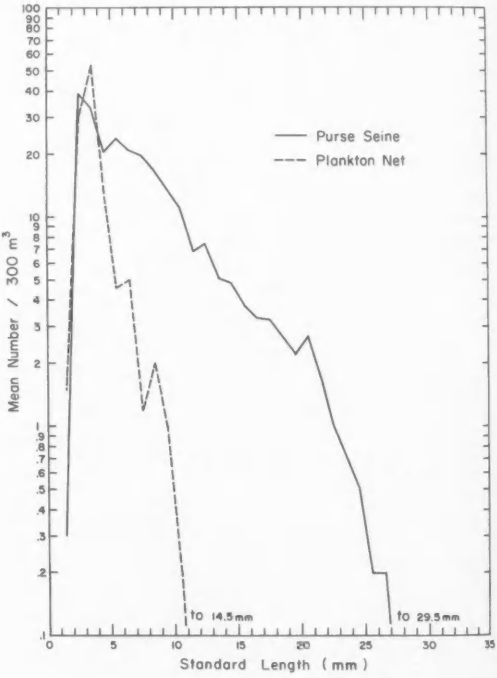

FIGURE 3.—Day catches of the purse seine and plankton net.

TABLE 1.—Results of paired purse seine and 1-m plankton net samples expressed as numbers per 300 m³. Lengths are preserved lengths. There were 44 paired samples.

Standard length (mm)	Day		Night	
	Purse seine	Meter net	Purse seine	Meter net
1.5	0.3	1.5		
2.5	39.3	30.7	13.3	
3.5	33.1	53.9	9.6	6.4
4.5	20.4	13.0	4.6	7.5
5.5	23.6	4.6	10.4	13.3
6.5	20.8	5.0	10.6	6.2
7.5	19.5	1.2	16.4	5.4
8.5	16.6	2.0	18.0	10.8
9.5	13.5	1.0	10.4	14.2
10.5	10.9	0.2	14.0	10.2
11.5	6.9	0.02	17.4	4.2
12.5	7.4	0.05	16.5	6.2
13.5	5.1	0.08	9.0	6.3
14.5	4.8	0.05	5.2	11.0
15.5	3.8		6.1	7.3
16.5	3.3		7.9	4.6
17.5	3.2		2.6	3.5
18.5	2.7		2.6	1.7
19.5	2.2		1.9	1.7
20.5	2.7		2.5	0.3
21.5	1.7		3.4	0.2
22.5	1.0		1.5	
23.5	0.7		1.7	
24.5	0.5		2.0	
25.5	0.2		3.8	
26.5	0.2		5.2	
27.5	0.02		5.6	
28.5	0.03		4.1	
29.5	0.02		2.3	
30.5			4.5	
31.5			1.1	
32.5			1.2	
33.5			1.2	
34.5			0.7	
35.5			1.7	
36.5			0.6	
37.5			0.8	
38.5			0.2	
39.5			0.2	
40.5			0.1	
41.5			0.1	
45.5			0.1	
Total	244.47	113.30	219.9	121.0

be accompanied by behavioral changes, e.g., onset of schooling, as well as more efficient swimming—all of which might increase their ability to escape the purse seine. The low numbers in the 1.0 to 2.0 mm (preserved lengths) are, at least in part, a function of the newly hatched larvae being able to pass through the 333 μ Nitex. The seeming differences in the next two larger intervals are not statistically significant (P = 0.216 and 0.141, respectively). The remainder, involving larvae greater than 4.0 mm, are all significant at the 0.01 level or greater.

NIGHT SAMPLES

The night samples (Table 1, Figure 4) were fewer in number (10) and, therefore, exhibit greater variance. They also suffer from poor stratification as evidenced by the near lack of a negative slope below 12 mm in length, in spite of what must be a very high mortality rate (see Figure 3). These data clearly indicate that the purse seine is superior at night too, even with respect to the smaller sizes, supporting Ahlstrom's (1954) contention that larvae probably dodge nets at night as well as day. For example, over the interval 3.5 to 11.5 mm, inclusive, the purse seine took 127.9 per 300 m³, and the meter net took only 69.8. Over a larger interval (3.5-19.5 mm), the purse seine took 163.2 larvae and the meter net 99.6. For this interval the F ratio is 6.19 with 1 and 32 df ($P < 0.025$). Never-

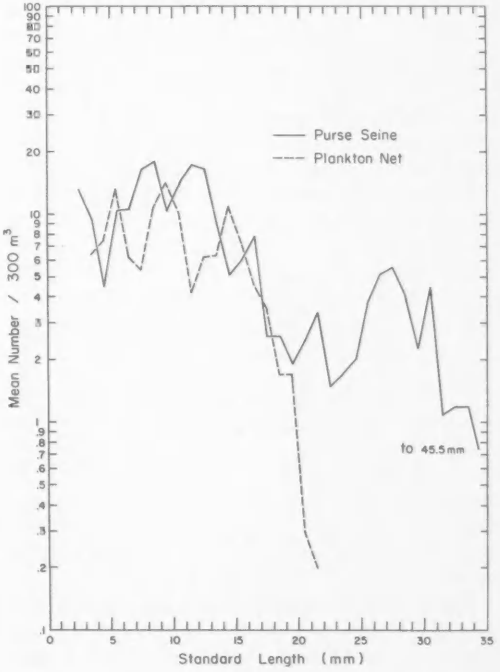

FIGURE 4.—Night catches of the purse seine and plankton net.

theless, the plankton net appears to be more efficient at night than during the day. The catches of the smaller larvae are closer to the purse seine catches than during the day, and much larger larvae were taken at night—21.5 mm maximum versus 14.5 mm by day. This suggests that vision plays an important role in dodging.

It is interesting to note that the maximum size taken by the plankton net at night (21.5 mm) coincides with a change of slope of the day purse seine catches. The plankton observation taken by itself might be interpreted as a size beyond which all larvae can swim out of the net even if they blunder into it. A length of 21.5 mm is approximately the size of metamorphosis and the onset of schooling. This social trait might also adversely affect the day purse seine catches to the extent that a school is more effective than the sum of the individuals in detecting and responding appropriately. It does not seem to have affected the night catches. This may be evidence that schools tend to disperse at night.

Each night station was paired with a day station. These latter were taken late in the afternoon at the same geographical point, but of necessity, several hours before the night station. Examination of the data shows that this degree of control was inadequate to allow meaningful comparisons, at least on the basis of only 10 sets of data.

A DODGING MODEL

In this section an attempt is made to rationalize the difference between the day plankton net catches and the day purse seine catches on the basis of the geometry of the towed net situation, the swimming speed of the larvae, and the alarm distance, i.e., the distance in front of the net that a larva would have to begin evasive action in order to avoid capture.

The algebra of the model is an extension of the results of Barkley (1964). We start with his equation (7) (our 1) which defines the escape velocity, i.e., swimming speed, necessary to escape a net assuming the larva is mathematically inclined and rational and, therefore, selects the shortest possible escape path. We follow Barkley's notation.

$$u_e = U\left[1 + \frac{x_0^2}{(R - r_0)^2}\right]^{-1} \quad (1)$$

where: u_e = escape velocity (swimming speed) (cm/sec)
U = towing speed of net (cm/sec)
x_0 = reaction distance of the larva (cm)
r_0 = initial offset of larva (from dead center of the net) (cm)
R = radius of net (cm).

Equation (1) can be rearranged to provide the minimum r_0 from which escape is possible given a swimming speed u_e yielding:

$$r_0 = R - [x_0 u_e (U^2 - u_e^2)^{-1}]. \quad (2)$$

Of course, escape is possible from all larger r_0's.

Now the proportion that escapes (P) is from elementary principles:

$$P = (\pi R^2 - \pi r_0^2)(\pi R^2)^{-1} \quad (3)$$

Substituting the right hand side of (2) into (3) and rearranging yields the desired equation, i.e., an expression relating the proportion escaping to swimming speed and alarm distance as follows:

$$P = \left[R - \left(\frac{x_0 u_e}{U^2 - u_e^2}\right)\right]^2 R^{-2}. \quad (4)$$

From (4) we can define the proportion caught (P') as simply $1 - P$. Assuming that the purse seine catches all larvae up to 10.5 mm by day, the proportion caught (or escaping) can be estimated as a function of size. The towing speed of the net was about 1.5 knots (76 cm sec^{-1}). This leaves two unknowns, alarm distance (x_0) and swimming speed (u_e). Our approach in testing the model is to estimate swimming speed as a function of size based on values in the literature, and solve for alarm distance—also as a function of size. As will be seen, the derived alarm distances seem intuitively reasonable and, anticipating a later section, may explain the relatively small increase in sampling power of larger towed nets.

Appropriate measurements on the swimming speed of larval anchovies are not available. What

are required are maximum sustainable speeds over distances ranging from 0 to 100 cm or so. Houde (1969) found that yellow perch larvae larger than 9.5 mm could sustain speeds up to 4 body lengths per sec for 1 hr. Larimore and Duever (1968) observed swimming speeds over 10 body lengths per sec for over 3 min for smallmouth bass 20-25 mm in length. Hunter and Zweifel (1971), Figure 4, present data for sustained swimming of jack mackerel 4.5-27.0 cm for short periods. These data fitted to the expression $y = ax^b$ yielded an a of 18.06, b of 0.829, and r of 0.997, y being speed in centimeters per second, and x body length (L) in centimeters. This gives an extrapolated speed of 10 cm per sec for a 5-mm nehu larva. More recently, Hunter (1972) observed burst speeds of very short duration as high as 28 lengths per sec for a 4.2-mm larva and 25 lengths per sec for a 12.1-mm larva. Whether such speeds can be sustained long enough to explain plankton net avoidance is not known. In the computations to follow, we assume that they can be sustained as follows. One trial (u_e') assumes that the backward extrapolation of the data by Hunter and Zweifel (1971) holds (cm/sec = $18.06\ L_{cm}^{0.829}$), and the second trial (u_e'') assumes that cm/sec equals body length in centimeters times 10.

The catch data were processed as follows. The raw data (second and third columns in Table 2) were fitted to exponential expressions (fourth and fifth columns). The purse seine data were then multiplied by 46.883/29.685 to adjust the data to the point of assumed 100% meter net efficiency (see Figure 2). P', the fraction retained, was then calculated as $1 - P$. u_e' and u_e'' were then calculated from the expressions in the preceding paragraph. Minimum alarm distance, x_0, was then calculated from:

$$x_0 = \frac{R(U^2 - u_e^2)^{1/2}\,[1 - (P')^{1/2}]}{u_e} \qquad (5)$$

which is a straightforward rearrangement of equation (4). The resulting minimum alarm distances (last two columns in Table 2) do not seem unreasonable. For example, it seems reasonable that a 7.5-mm larva could detect a meter net 200-400 cm away and begin to take meaningful evasive action. The greater effectiveness of towed nets at night might be caused by a reduction in detection distance as well as reduced ability to take early, well-directed evasive action.

OTHER TOWED NETS

Two additional sets of data will be considered here. The first is a comparison between a 10-ft Isaacs-Kidd trawl and a standard meter net. The ratio of mesh area-to-mouth opening was the same for both nets in order to ensure comparability of hydrodynamic and clogging characteristics. The trawl was meshed throughout with Nitex having an opening of 0.505 mm. This is nearly the same as that used in the standard CalCOFI (California Cooperative Oceanic Fisheries Investigations) meter net which, according to Smith, Counts, and Clutter (1968), had silk gauze with a mesh width of 0.55 mm as its main

TABLE 2.—Calculation of escape parameters for meter net and purse seine data.

Standard length (mm)	Purse seine observed	Meter net observed	Purse seine calculated[1]	Meter net calculated[2]	Purse seine adjusted[3]	P'	u_e'*	x_0'†	x_0''†
3.5	33.082	53.905	29.685	46.883	46.883	1.000	7.564	0	0
4.5	20.366	12.984	26.063	19.754	41.163	.4799	9.316	134.7	288.7
5.5	23.575	4.627	22.883	8.323	36.140	.2303	11.002	190.6	397.0
6.5	20.807	5.048	20.091	3.507	31.731	.1105	12.637	210.3	428.1
7.5	19.507	1.157	17.639	1.478	27.858	.0531	14.228	212.6	424.6
8.5	16.616	2.048	15.847	.623	25.028	.0249	15.7837	207.0	407.0
9.5	13.457	1.034	13.597	.262	21.474	.0122	17.3082	196.9	381.8
10.5	10.941	0.018	11.938	.111	18.854	.0059	18.8054	185.6	355.8

[1] P.S. $Y = ae^{bx}$ $r = -.93779$ $b = -.13013$ $a = 46.81074$ x = length (mm).
[2] M.N. $Y = ae^{bx}$ $r = -.90039$ $b = -.86431$ $a = 965.5874$ x = length (mm).
[3] P.S. calculated × 46.883/29.685.
* $u_e' = 18.06\ L\ (\text{cm})^{0.82896}$; $u_e'' = 10\ L$ (cm).
† $x_0 = \dfrac{R\,(U^2 - u_e^2)^{1/2}\,[1 - (P')^{1/2}]}{u_e}$.

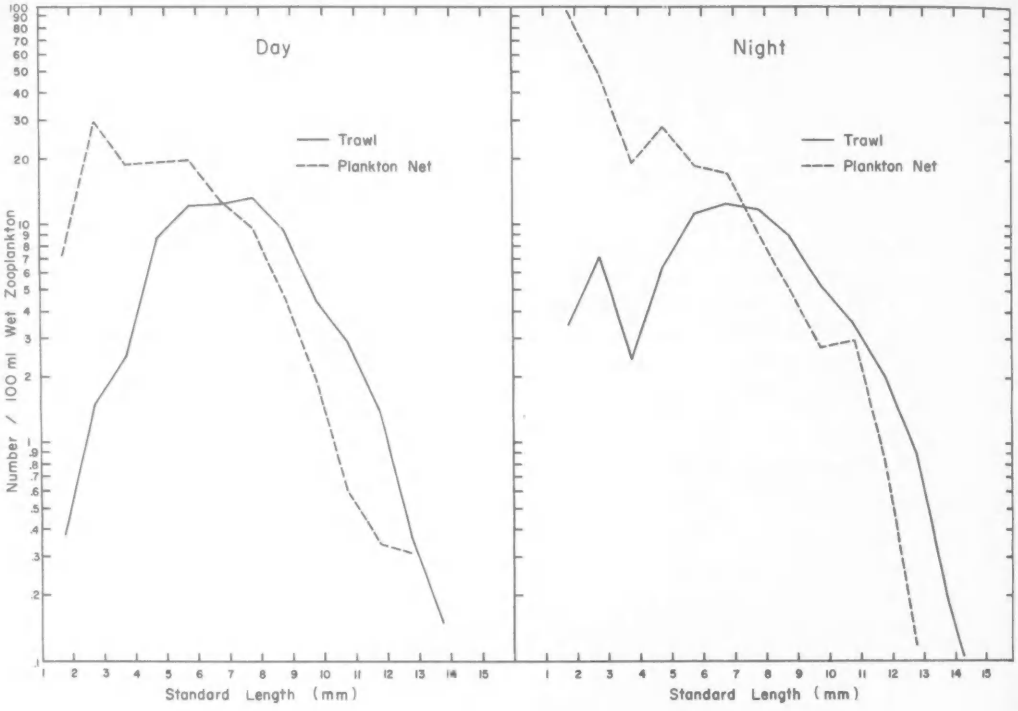

FIGURE 5.—Day and night catches of the Isaacs-Kidd trawl and the standard CalCOFI meter net.

body. It had a porosity of 36% after use compared to 51% for the Nitex. For this reason, the trawl, though preserving the geometry of the meter net, has a slightly better filtering capacity. These two nets were alternated over replicate courses off southern California during the period May 6 to May 8, 1964. In all, there were 22 paired day samples (½-hr tows) and 10 paired night samples.

The trawl-plankton net series are compared in Table 3 and Figure 5. The results are expressed as numbers per 100 ml of wet plankton taken. This was thought to be the best way to control the catches between the unmetered trawl and the metered plankton net. The severe undersampling of the small larvae by the trawl has no ready explanation, but could have been caused by our inadvertently having to tow at a faster speed in order to maintain the vaned trawl at proper towing depths or by the greater transparency of the Nitex, which would reduce the effect of partial clogging on effective mesh size. The trawl is about twice as effective as the plankton net (Table 3) in the capture of larvae over 8.75 mm in length by day, but only slightly more efficient at night. With respect to both day and night, the trawl falls far short of the purse seine both with respect to the increased catches of larger larvae and the extension of upper limit of capture. The latter, of course, might be ascribable to the absence of larger larvae at the California sampling stations, but this seems unlikely.

The mean escape radius for the trawl is 3.4 times that of the meter net and led us, a priori, to expect a much greater enhancement of the

TABLE 3.—Summary of the meter net and trawl catches of anchovy larvae off southern California, May 6-8, 1964. The data are in numbers per 100 ml of wet volume zooplankton taken.

Length (mm)	Day		Night	
	Meter net	Trawl	Meter net	Trawl
1.75	7.332	0.382	96.160	3.490
2.75	28.746	1.491	48.030	7.110
3.75	18.869	2.473	19.360	2.430
4.75	19.320	8.619	28.060	6.410
5.75	19.927	12.222	18.880	11.200
6.75	12.860	12.578	17.130	12.480
7.75	9.646	13.168	9.070	11.890
8.75	4.650	9.432	5.020	8.880
9.75	1.959	4.537	2.760	5.260
10.75	0.604	2.887	2.960	3.590
11.75	0.345	1.428	0.840	2.020
12.75	0.313	0.368	0.120	0.900
13.75	--	0.150	--	.190
14.75	--	--	--	.060

TABLE 4.—Catches of four replicates of the purse seine and three simultaneously towed nets. Numbers are per 300 m^3 of water strained.

Length (mm)	Purse seine	1-m net	½-m net	¼-m net
2.5	1,289.8	689.3	278.6	95.7
3.5	296.6	1,122.7	686.2	217.9
4.5	156.8	152.0	67.9	35.8
5.5	81.0	20.6	26.7	8.2
6.5	135.4			
7.5	89.5			
8.5	129.5			
9.5	49.3			
10.5	31.1			
11.5	29.6			
12.5	25.3			
13.5	41.4			
14.5	9.3			
15.5	10.1			
16.5	17.4			
17.5	2.6			
18.5	1.7			
19.5	6.9			
20.5	10.9			
21.5	7.8			
22.5	10.1			
23.5	8.3			
24.5	4.9			
25.5	0.9			

catches. Perhaps the larger size is detected farther away (increased x_0), cancelling most of the advantage. This suggests that a towed net has to be large enough not to be perceived as a meaningful whole in order to significantly increase the catches of efficient escapers such as the anchovy.

The final set of data to be considered is four sets of stratified (in the same way as the purse seine-meter net data) samples taken by purse seine, 1-m net, ½-m net, and ¼-m net. All four sets were obtained on August 25, 1967, during daylight. The results (Table 4), apart from again demonstrating the superiority of the purse seine, are somewhat ambiguous. The towed nets clearly show a dramatic decrease in efficiency with decreasing size in terms of numbers caught, but the also-to-be-expected increase in slope (negative) with decreasing net size is not apparent.

The total numbers caught by the three towed nets are approximately proportional to the mean escape distance, but this observation is at variance with the slight improvement associated with the 10-ft trawl compared to the meter net discussed earlier. Very possibly the inconsistencies are a function of the limited sampling, especially with respect to this last set of data.

DISCUSSION

Clutter and Anraku (1968) thoroughly reviewed the dodging problem on the basis of evidence and literature then available. Many of the data they reviewed were contradictory, and to some extent, we have extended the library of contradictions in this paper. We have, however, clearly shown from our purse seine data that towed nets are rather inefficient as samplers of at least one kind of fish larvae (anchovy)—especially by day. Likely, this conclusion can be extended to other pelagic larvae, as there must surely be strong selective pressure for avoidance of predation.

The algebraic model developed to reconcile the difference between our day purse seine and meter net catches involved two parameters, escape speed and alarm distance. It may be that future experimental work will not sustain the assumed escape velocities. If not, either a new model must be invoked or the alarm distance must be increased. The transparency of the water in Kaneohe Bay is low, so a very great extension of alarm distance on the basis of vision is not intuitively attractive.

A great deal of work has been directed at the design of towed nets in order to clean them up with respect to their disturbance in the water

and, hence, the vigor with which they telegraph their arrival. Yet, the dramatic improvement in the efficiency of towed nets at night suggests that vision is the most important avoidance cue. But, the optical characteristics of sea water are such that objects become invisible through contrast attenuation rather than resolution attenuation. This being so, large nets such as the Isaacs-Kidd trawl should be sighted at nearly the same distance as smaller nets such as the meter net. There should, then, be a dramatic increase in effectiveness with size. This is not evident in our data or anyone else's.

Short of resolving these contradictions, it appears that the development of towed sampling devices should proceed, as suggested by Clutter and Anraku (1968), in the direction of larger size, greater speed, and invisibility. The large scale "grab" sample, of which our purse seine is a rather specialized example, appears to be a possible definitive solution, or at least a practical means of calibrating towed nets.

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SELECTIVITY OF TOWED-NET SAMPLERS

RICHARD A. BARKLEY[1]

ABSTRACT

The ideal sampler for plankton and nekton is one whose selective characteristics are known to be appropriate to any given problem, so that it catches the right organisms, and rejects others, with known efficiency. This paper presents a quantitative theoretical analysis of one aspect of selectivity, avoidance of towed-net samplers. The theory is evaluated against three sets of paired samples obtained by different nets at different speeds to provide absolute and relative tests of its validity. A single sample obtained by one net towed at one speed is then analyzed to illustrate the procedure. Final evaluation of the theory awaits studies of animal behavior when confronted by a sampler, but the theory provides informative and reasonable interpretations of plankton and nekton catch data, particularly estimates of population abundance and mesh losses, even when behavior of the animals is not known.

An ideal sampler for plankton and nekton must meet at least two requirements, one qualitative and the other quantitative: It must collect or detect certain components of these extremely diverse communities, while rejecting most others; and it must do this with known effectiveness. For some purposes the qualitative aspects of sampler selectivity are relatively more important than the quantitative ones, or vice versa, but neither can ever be completely ignored in the design and selection of sampling gear.

Sampler selectivity has usually been evaluated empirically, by comparing results obtained with one sampler under different conditions or by intercomparing various sampling methods. The plankton purse seine developed by Murphy and Clutter (1972) appears to be nearly ideal for the latter purpose. It is relatively nonselective for a wide spectrum of organism types and sizes, making it useful as a "primary standard" for calibrating more selective gear, as Murphy and Clutter demonstrate.

A sound theory of sampler selectivity would be of great value as a guide to the collection and analysis of empirical data, but relatively little effort has been devoted to the development of such theory (Tranter, 1968). What I propose to discuss here is a special, rather basic, case of selectivity: the theoretical minimum probability of certain capture, for many individual encounters between similar organisms and a towed-net sampler.

The formulation of this problem was suggested by the work of Murphy and Clutter (1972). The results resemble those obtained by Gilfillan (reported by Clutter and Anraku, 1968) but are more general. This study is an extension of my earlier theoretical work on net avoidance (Barkley, 1964) and uses the same notation.

This paper is presented in recognition of the inspiration and leadership of Oscar Elton Sette. It is appropriate that it should appear just one century after the first worldwide use of the Müller net on the *Challenger* Expedition.

METHOD

Consider a towed-net sampler moving through the water toward an individual animal (Figure 1a); for simplicity assume that the net has a circular opening of radius R and moves at a constant speed U. The animal senses the oncoming net and begins to react to it at a distance x_0, by swimming at some mean escape speed u_e. In the time available before the net catches up, the animal either can, or cannot, get out of the way, depending on its position, speed, and di-

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rection of movement relative to the net. There is, therefore, a cone-shaped space ahead of the net which, once it encloses the animal, results in certain capture. If the animal reacts before entering the (invisible) "lethal cone," it has enough time to get out of the way of the oncoming net. The base of this "lethal cone" is the opening of the net; its apex is at a distance X ahead of the net. This distance, X, is given by the equation:

$$X = R\sqrt{\frac{U^2}{u^2_e} - 1} \qquad (1)$$

which is easily obtained from the following equation (Barkley, 1964) by setting $r_0 = 0$ and $x_0 = X$:

$$u_e = \frac{U}{\sqrt{1 + \frac{x^2_0}{(R - r_0)^2}}} \qquad (2)$$

Figure 1 (panels a and b) gives examples of the "lethal cone" for several values of escape speed relative to net speed. For organisms which do not react to the net ($u_e = 0$) or have very low escape speeds the "lethal cone" is very large, occupying all or almost all of the volume of water in the path of the net; the probability of capture for such organisms approaches 1.0. On the other hand, for animals whose escape speed approaches the speed of the net ($u_e \simeq U$) the "lethal cone" is short; these animals can easily dodge the oncoming net, even if they wait

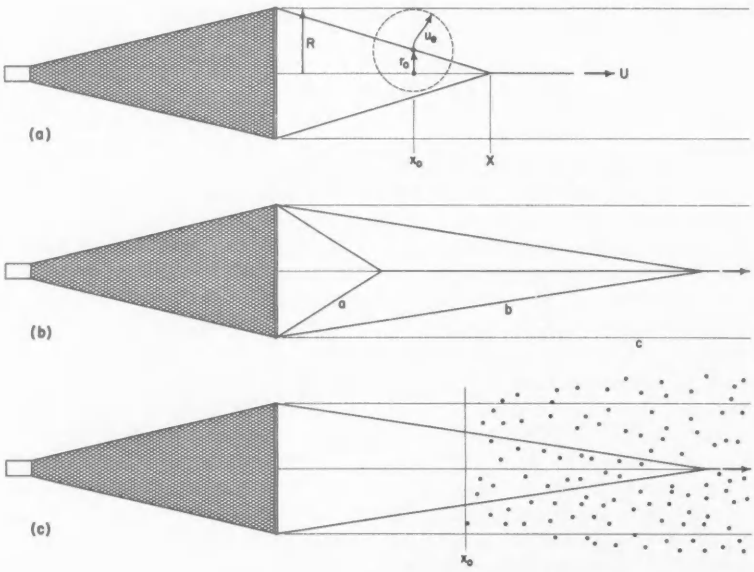

FIGURE 1.—(a) An animal at a point x_0 ahead of the net and r_0 from its axis of motion begins to react to the net. In the time available, it can go anywhere within the volume shown in dashed lines; if this volume is completely enclosed by the oncoming net, capture is certain. Animals which react before entering the cone-shaped space ahead of the net can escape; those which react after entering the "lethal cone" are caught. (b) For a given net, the length of the "lethal cone" depends only on the speed of the animal relative to the net. Cone a corresponds to animals which can move at 50% of the net's speed. Cone b represents a relative speed of 15%; cone c shows the case of no reaction. The "lethal cone" in panel a, above, corresponds to a relative speed of 30%. (c) If a school or cluster of animals reacts to the dodging movements of the animals nearest the oncoming net, only those animals already inside the "lethal cone" are certain to be captured.

until the net has almost caught up with them. We do not expect to catch any animals which can swim faster than the net; we wish to calculate minimum probabilities for certain capture, which implies that animals which could possibly escape do so. That is, the size of the "lethal cone" is minimized by assuming that animals are capable of optimum avoidance behavior.

However, probabilities of certain capture can only be calculated for animals which react individually. Animals which school or form clusters can "beat the odds" by reacting to each other's behavior instead of reacting only to the oncoming net. The effect of this is illustrated in Figure 1c, which represents a net approaching a group of animals whose reaction distances and escape velocities are assumed to be similar. If the animal shown nearest the net begins to react at the distance labeled x_0, it can escape because it is outside of the "lethal cone." Those animals already within that cone will be captured in any case. If the other animals respond immediately to the actions of the one nearest the net, they can all escape. If, instead, they respond as individuals, as the net moves through the group, more will enter the "lethal cone" and then be captured.

Whether an organism, once captured (i.e., enclosed by the net) will be retained depends on the characteristics of the net's meshes and the size, shape, behavior, and fragility of the organism. Losses through the mesh have been reviewed by Heron, 1968; Tranter and Smith, 1968; and Vanucci, 1968. Lenarz (1972) presents results of more recent work. Losses can also occur due to faulty handling of the sampler, particularly sudden decreases in towing speed. Our primary interest here is in avoidance prior to capture, although the theory to be developed will throw some light on the problem of mesh losses.

The catch obtained from a towed-net sampler can be calculated, in principle, from equations such as the following:

$$\text{Catch} = \text{Captures} - \text{losses}$$

$$= (\text{volume sampled}) \times \left(\frac{\text{no. of organisms}}{\text{unit volume}}\right) \times (\text{probability of capture}) - (\text{losses}) \quad (2)$$

So that

$$\frac{\text{no. of organisms}}{\text{unit volume}} = \frac{(\text{catch} + \text{losses})}{(\text{volume sampled}) \times (\text{probability of capture})} \quad (3)$$

The central problem of selectivity theory is to evaluate the unknown factors in equations (2) and (3), so as to permit solution of these equations with a minimum of empirical work. The most important unknown factors are those governing probability of capture and losses after capture—primarily losses through the meshes.

Since both probability of capture and degree of mesh loss must vary widely with species, age, and condition, the above equations apply separately to each component of the plankton and nekton community.

For present purposes, a component must be defined as a set of organisms having the same probability of capture, and the same degree of mesh retention, under given circumstances. That is, they must be similar in their reaction distance, escape speed, shape, size, and condition.

The above operational definition of a component of the plankton or nekton may often coincide with the more usual biological definitions. For single species, one can reasonably expect that fish of similar size or crustaceans at the same stage of development should have similar reaction distances and escape speeds and the same percentage mesh retention. However, the distinction between the two ways of defining a component must be carefully borne in mind. The operational definition may lump several biologically defined components; to take a trivial example, bacteria, phytoplankton, and fish eggs small enough to pass through the mesh all have the same probability of capture, 1.0, and all have 0% retention. On the other hand, the operational definition may split one biological component into two or more parts; e.g., healthy and moribund animals of the same size and species should differ in their ability to avoid capture. In principle, empirical data on reaction distance,

escape speed, shape, size, and condition are needed to assign animals to different components when analyzing towed-net samples by means of the present theory. Such data could perhaps best be obtained by taking stereoscopic photographs of animals' reactions to the approach of a sampler. In practice, however, it may be possible to assign animals to operationally defined components *post facto*, based on analyses of catch data with the present theory. An example of this is to be found in Table 1, where *Bathylagus stilbius* ranging from 52 to 92 mm in length were found to have essentially identical probabilities of capture and were apparently all retained by the meshes, thus meeting the criteria for a single component.

In equations (2) and (3) the major unknowns are the losses and the probability of capture. Neither can be formulated precisely until behavior of many animals, before and after entering nets of varied designs, has been studied. However, losses can be estimated to some degree from the difference between observed and theoretical catches; and probability of capture can be calculated for a limiting case, minimum probability of certain capture for individual encounters. This approach makes use of the geometry of the "lethal cone" (Figure 2). The minimum probability of capture, P_c, is:

$$P_c = \frac{\text{Area of "lethal cone" cross section at distance } x_0}{\text{Area of the sampler mouth opening}}$$

$$= (r/R)^2.$$

From Figure 2,

$$\frac{R - r}{x_0} = \tan \alpha = \frac{R}{X}$$

so that

$$r = R(1 - \frac{x_0}{X})$$

and

$$P_c = (1 - \frac{x_0}{X})^2. \quad (4)$$

Substituting X from equation (1) into (4) gives

$$P_c = \left(1 - \frac{x_0}{R\sqrt{\frac{U^2}{u_e^2} - 1}}\right)^2 \quad (5)$$

which may also be written

$$P_c = \left(1 - \frac{x_0 u_e}{R\sqrt{U^2 - u_e^2}}\right)^2 \quad (6)$$

Where P_c is probability of capture, x_0 is the mean reaction distance, R is the radius of the net's opening, U is the net's speed, and u_e is the animals' mean escape speed. These results can also be derived from equations (4), (5), and (7) of my earlier analysis (Barkley, 1964).

DISCUSSION

To examine avoidance as a function of towing speed, Gilfillan (reported by Clutter and Anraku, 1968) assumed that the product $x_0 u_e$ is a constant, K. Starting with an apparent "effective"

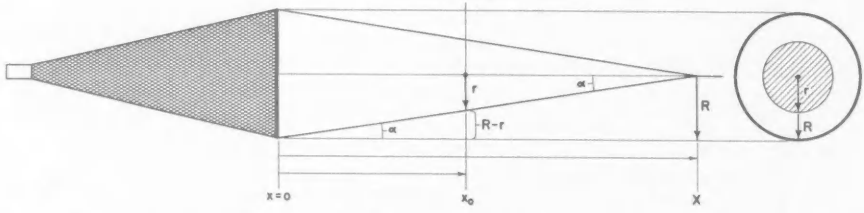

FIGURE 2.—Definition sketch for calculating P_c, the minimum probability of capture. P_c is the ratio of the area of the "lethal cone" (shaded) to the area of the net's mouth opening, at the mean reaction distance x_0 for one component of the catch.

net radius R' (identical with r in Figure 2), Gilfillan arrived at the following equation:

$$P_c = \left(1 - \frac{K}{RU}\right)^2, \qquad K = x_0 u_e \quad (7)$$

where present notation has been substituted for the original and the equation slightly simplified. Clearly Gilfillan's equation is an approximate form of equation (6) for the case where u_e can be neglected compared to U; which is to say, for animals which move much slower than the net. This approximation is good to within 5% as long as u_e is less than 30% of U.

It is not obvious that $x_0 u_e$ should in general be a constant, even for a single component of the plankton or nekton. Constancy of the product $x_0 u_e$ implies that either (1) reaction distance and escape speed individually are constant, (2) animals deficient in one of these survival traits can compensate for this by excelling in the other, or (3) animals given an unusually long time to react by faulty net design—such as a bridle or other conspicuous obstruction some distance ahead of the mouth—fail to take advantage of this warning. The first alternative is perhaps too much to expect; the second and third seem unlikely. Nevertheless, Gilfillan obtained nearly constant values for K in a series of field trials with different nets towed at various speeds, where catches of *Calanus* spp., *Euchaeta japonica*, and euphausiids were enumerated (Clutter and Anraku, 1968).

There is great practical value to knowing that K is a constant for any particular component of a sample, because this constant fully specifies the avoidance behavior of that component. If K is constant, it is possible to calculate probabilities of capture without making measurements of either x_0 or u_e, as long as U is known to exceed u_e by a factor of three or more.

Numerical values of K can be estimated, as Gilfillan suggested, from tows made at two different speeds, U_1 and U_2, or by using two otherwise similar nets with openings of radii R_1 and R_2, while holding other factors constant:

$$K = \frac{1 - \left(\frac{C_1}{C_2}\right)^{1/2}}{\frac{1}{R_1 U_1} - \frac{1}{R_2 U_2}\left(\frac{C_1}{C_2}\right)^{1/2}} \quad (8)$$

where C_1/C_2 is the ratio of catches of individual components in the samples taken under each of the two different conditions. Equation (8) is approximate; the exact form can be obtained by substituting $\sqrt{U^2_n - u^2_e}$ for U_n.

Holding "other factors" constant is obviously a problem, since the same net towed at different speeds, or different size nets towed at the same speed, may have widely different noise levels, mesh losses, hydrodynamic behavior, etc., which would tend to invalidate the comparison.

RESULTS

Although definitive tests of the theory developed above must await knowledge of avoidance and mesh escape behavior of at least some components of the plankton and nekton, a few informative comparisons can be made now between theory and catches obtained with various towed nets.

Equation (5) is presented graphically in Figure 3, where P_c, the minimum probability of capture (ordinate) is plotted as a function of the ratio u_e/U, the escape speed relative to the net's speed, for various values of the ratio x_0/R, the reaction distance relative to the net's radius. The linear graph shows the complete theoretical solution; it is used to provide a check on results obtained using the semilog format. In practice the semilogarithmic graph is more useful for analyzing catch data because it simplifies graphical calculations. Either of these graphs, as well as equations (5), (6), and (7), can of course be used to determine P_c, u_e, or x_0 if any two of these variables are known, along with R and U. For example, a 1-m net ($R = 0.5$ m) towed at 100 cm/sec should catch at least one-third ($P_c = 0.33$) of all those organisms in its path which react at a distance of 1 m and can swim 20 cm/sec ($u_e/U = 0.2$, $x_0/R = 2$).

A more interesting application is the use of Figure 3 to analyze size-frequency data from a tow, or set of tows, made with one sampler at one speed. To illustrate this application, suppose that the population in question is a species for which mesh losses are negligible beyond some

minimum size or stage of development and that the species' abundance does not change appreciably with size, or that corrections can be made for these two factors. Assume that the species' swimming ability is known, and proportional to size, while its reaction distance remains constant, or nearly constant, for all sizes sampled. Then if the catch were sorted into size class intervals (ideally, into components, in the operational sense) and counted, the size classes could each be assigned a corresponding escape speed, increasing with size; plotting these speed-frequency values as points on either graph of Figure 3 would produce a curve which resembles one of the family of curves shown on those graphs. Proper matching of observed data to the theoretical curves would yield unique values of both P_c and x_0/R (and therefore x_0, since R is known) for each component or class interval of that species. Once P_c is known, the absolute population density can be calculated from equation (3). Finally, values of x_0, or x_0/R, provide valuable information as to the relative merits of different sampler designs.

The following examples illustrate this use of avoidance theory. In the first example, the population density structure is known, so that P_c can be calculated directly and only x_0 remains to be determined from avoidance theory. In the second example, two different samplers are compared to obtain estimates of P_c and x_0 for both, from the theory, even though the population structure is not known. The third example illustrates information which can be obtained when one sampler is towed at two different ranges of speed. Finally, catch data from a single net, towed at one speed, are considered.

Murphy and Clutter (1972) present length-frequency data for Hawaiian anchovy, the engraulid, *Stolephorus purpureus*, caught with their plankton purse seine and a 1-m net. Their data for paired daylight tows are reproduced on Figure 4. The uppermost curve on this figure shows length-frequency data from the purse seine, assumed to represent the population structure as a function of size. I approximate these data by means of the straight line shown on this figure, in effect assuming that the population declines exponentially as the fish grow to larger sizes. That is, $N_L = N_0 \exp(-kL)$, where N_L is the population density at length L, N_0 is a fictitious population density at zero length obtained by extrapolation, and k is a constant. The lowest curve on Figure 4, marked C_L, shows the catch (C) in each 1-mm length class (L).

To remove the effects of changes in population density, set $N_0 = 1.0$ by dividing all values of N_L by the population density at N_0. On semilog graph paper this can easily be accomplished simply by aligning N_0 with 1.0 on the ordinate scale, after the length-frequency values have been plotted on tracing paper using the three-cycle semilog scale of Figure 3. Next, divide each value of C_L by the corresponding value of N_L to obtain the middle curve of Figure 4, labeled C_L/N_L. This division can be performed graphically by moving each value of C_L vertically upward a distance equal to the vertical distance between N_L at the corresponding length, L, and the horizontal line $P_c = 1.0$. This procedure yields the length-frequency curve which would have been obtained if the population density in each class interval had been the same, i.e., $N_L = N_0$.

The above procedure amounts to dividing catch per unit volume by the population per unit volume, which according to equation (2) yields

$$\frac{\text{Catch/unit volume}}{\text{No. of organisms/unit volume}} = \text{Probability of capture (if losses} = 0).$$

Thus the curve labeled C_L/N_L on Figure 4 is also a curve showing P_c for each class interval, providing that catch per unit volume has been correctly related to the population per unit volume in each class interval and that mesh losses are negligible.

Mesh losses appear to be negligible for animals larger than the two smallest class intervals, which will not be used in the analysis. Since u_e is not known, length for each class interval is converted to escape velocity by assuming that $u_e = 10L$ where u_e is in cm/sec and L is in cm. Each value thus obtained is divided by U, nominally 76 cm/sec. Resulting values of u_e/U are shown in the upper abscissa of Figure 4. The

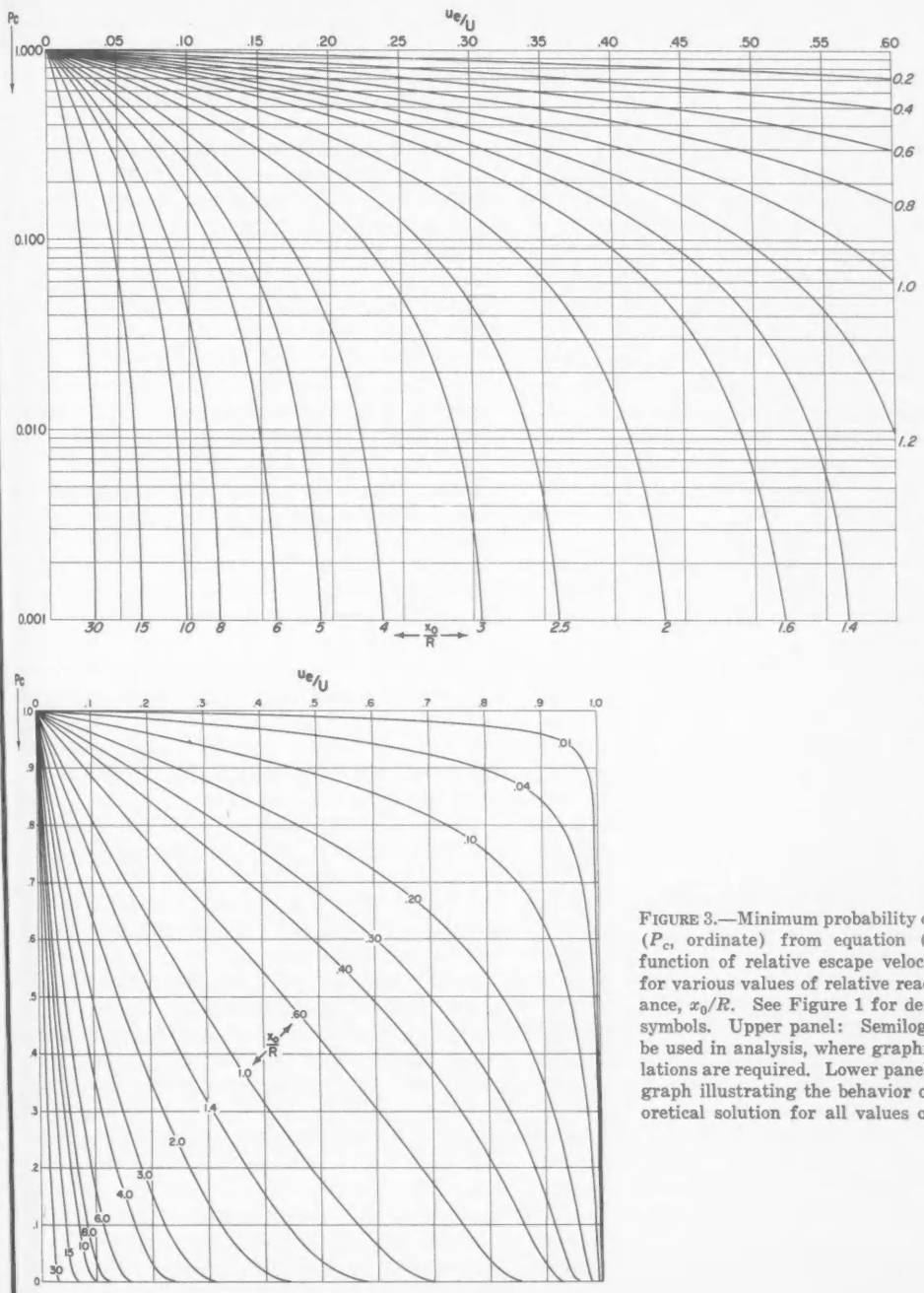

FIGURE 3.—Minimum probability of capture (P_c, ordinate) from equation (5), as a function of relative escape velocity, u_e/U, for various values of relative reaction distance, x_0/R. See Figure 1 for definition of symbols. Upper panel: Semilog graph to be used in analysis, where graphical calculations are required. Lower panel: Linear graph illustrating the behavior of the theoretical solution for all values of u_e/U.

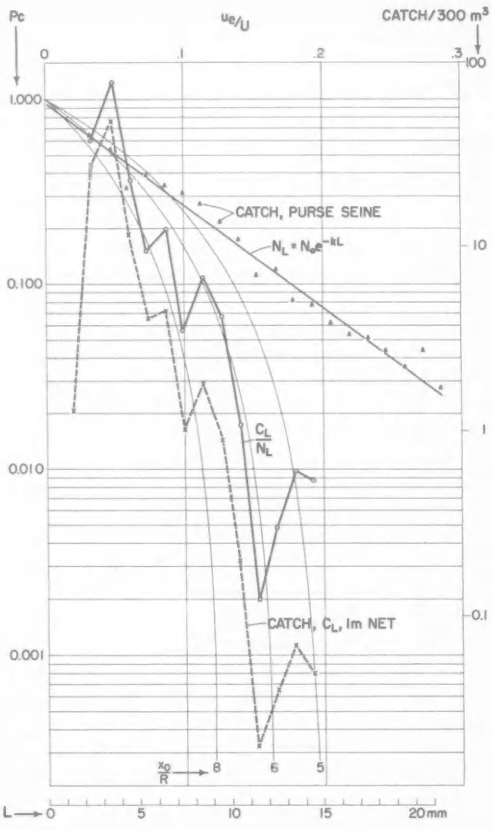

FIGURE 4.—Analysis of length-frequency data for daylight catches of *Stolephorus* from 44 paired samples. Purse seine data (triangles), a measure of absolute abundance, are approximated by the straight line, N_L. Catch with the 1-m net, C_L, has been corrected for changes in population (N) with length (L), to obtain the middle curve, C_L/N_L, which shows the minimum probability of capture, P_c, as a function of length for the 1-m net. Three theoretical curves for P_c at constant relative reaction distance (x_0/R) are reproduced from Figure 3, to show degree of fit between data and theory. Data from Murphy and Clutter (1972).

converted data can now be directly compared with the theoretical curves of Figure 3, three of which are shown on Figure 4 (the curves for P_c at $x_0/R = 5$, 6, and 8).

The adjusted 1-m net catch data fall near the theoretical curves for P_c at relative reaction distances, x_0/R, of 6 and 8; since $R = 0.5$ m for this net, the reaction distance of *Stolephorus* apparently ranges between 3 and 4 m. Murphy and Clutter (1972) obtain comparable results from an equation they derive for calculating x_0 directly. They used similar assumptions—in particular, an escape speed of $10L$ per second—but set $P_c = 1.0$ for the third class interval (3.5 mm). Here P_c was set at 1.0 at the intercept of the purse-seine catch curve with the ordinate axis, i.e., $P_c = 1.0$ at N_0, the fictitious population density at zero length, because only at this length does the assumed relationship between speed and length yield zero velocity. Since N_L, the population density at any given length L, is equal to N_0 for the adjusted data, the above procedure is internally consistent.

There are two exceptions to the otherwise fairly good fit between the adjusted data and the theoretical curves. The first, catch with P_c exceeding 1.0 for the third class interval (3.5 mm), may be due to sampling variability, overestimates of the water sampled by the purse seine, or underestimates of the water sampled by the 1-m net. It could also be due to less than optimum avoidance behavior by these small fish. The second exception, unexpectedly large catches in the three largest class intervals (12.5-14.5 mm) could be due to variability, or to a decrease in mean reaction distance for these animals, from a "normal" value of 3-4 m down to about 2.5 m ($x_0/R = 5$). Isaacs (1965) suggested that daytime tows should catch more than proportionate numbers of the sick, lame, or lazy; this effect should be most pronounced for the largest animals, which normally are the ones best able to dodge the net.

Minor fluctuations in the fit of the adjusted 1-m net data on Figure 4 are probably due to sampling variability, but to illustrate use of avoidance theory, suppose that the minor peaks and valleys for fish of intermediate sizes were significant. Note that these points tend to fall into two groups: those near the curve for P_c at $x_0/R = 6$, and others, $x_0/R = 8$. This could be an artifact due to schooling behavior, since group reaction should reduce the probability of capture below the theoretical minimum value for individual reaction. One measure of this effect

is an increase in the apparent reaction distance. Instead of the true value, x_0, we would expect to obtain an apparent value which approaches (x_0 + radius of the school) for large schools. If *Stolephorus* schools at all sizes represented on Figure 4, the different values of x_0/R, 6 versus 8, may reflect the presence of smaller and larger schools, differing in radius by about $2R$ or 1 m.

Some support for this apparently fanciful argument can be found in the *Stolephorus* catches obtained at night by Murphy and Clutter (1972). Night purse-seine catches showed marked peaks in abundance of fish in the 7-8 mm and 11-12 mm size classes and relatively low abundances in the 4- , 9- , and 14-mm class intervals. Simultaneous tows with the 1-m net, on the other hand, yielded precisely opposite results. The 1-m net apparently undersampled abundant size classes and was more effective with the less abundant size classes. This is precisely what is expected if the purse seine catches schools of various sizes equally well, whereas the 1-m net underestimates the abundance of schooled fish, more or less in proportion to school diameter, provided only that the fish school by size and that changes in abundance are associated with changes in school size, rather than changes in the number of schools.

This detailed treatment of a single set of length-frequency data is intended only as a demonstration of the amount of information which can be extracted from such observations in the light of theory, when and if measurements of typical reaction distances and escape velocities have been made. Results of this as-yet-tentative analysis may be summarized by saying that *Stolephorus* in the 1-m net sample apparently consist of:

A. Animals in the 1.5- and 2.5-mm class intervals, which are partially lost through the meshes and probably are unable to avoid the net.

B. Animals 3.5 mm long, which seem to be adequately retained by the meshes and apparently are too small to effectively avoid the net.

C. Animals 4.5 to 11.5 mm long, which react at about 3-4 m distance (proportionately more, or less, if their swimming speed is less, or more, than 10 body lengths per second). Maximum P_c for this group is about 0.35 for the 4.5 mm fish, dropping to 0.002 for the 11.5 mm fish.

D. Animals 12.5 to 14.5 mm long, which have anomalously large values of P_c when compared to group C, above. If these differences are significant, this implies that their reaction distances or swimming speeds, or both, may be abnormally low.

In the following examples there are no measurements of absolute abundance to compare with towed-net catch data, so assumptions will have to be made as to the relative contributions of population structure and avoidance to the outcome of sampling. Before making such assumptions it will be useful to consider the relative effects of these two factors in the case of *Stolephorus*.

On Figure 4 it can be seen that population abundance of *Stolephorus*, N_L, changed by a factor of 10 over the length interval sampled by the 1-m net. Over this same size interval the catch per class interval (C_L) changed by a factor of 1,000 or more. Thus N_L accounts for no more than 1% or 2% of the observed changes in catch length frequency, the remaining 98% to 99% being attributable to avoidance, at least for animals large enough to be fully retained by the mesh. In this strictly relative sense a 10-fold change in population density with size is in fact negligible, however important it may be in another context.

The problem of relative significance can be placed in perspective by considering whether data such as the 1-m net *Stolephorus* catches might be used to estimate population structure. Daylight 1-m net catches appear to be so overwhelmingly influenced by avoidance that even a 100-fold change in N_L might not be measurable since it could be obscured by a mere 10% error in estimating the effects of avoidance. In this sense it would be fair to assume that a population's structure is uniform, constant for all class intervals sampled by a given net if changes in N_L could not have been measured by that net. This can reasonably be taken to be true whenever the right-hand slope of the catch curves (C_L) exceeds the slope of the population curve

(N_L) by a factor of 10 or more, as it does in Figure 4.

When this assumption is made, however, it must be recognized that the results of any subsequent analysis are contaminated by whatever population structure effects are present and erroneously attributed to avoidance.

Anchovy (*Engraulis mordax*) larvae were also collected off southern California by Murphy and Clutter (1972) with a 1-m net and an Isaacs-Kidd midwater trawl (IKMT). Both nets had similar mesh size and were towed in daylight and at night at comparable speeds, nominally 75 cm/sec (although the IKMT may have been towed somewhat faster). Figure 5 shows data from these tows, converted to speed frequency by assuming that $u_e = 10L$. No estimates of absolute abundance were made for anchovy by Murphy and Clutter; the plankton purse seine was not used in these trials. However, Figure 4 shows that even 10-fold changes in N_L, abundance as a function of length, do not materially alter the shape of the *Stolephorus* speed-frequency curve. Essentially identical results could have been obtained by fitting the catch data to the theoretical curves without correction for changes in population density. Since anchovy are in many ways similar to *Stolephorus*, it may be tentatively assumed that avoidance is the major determinant of size-frequency curves for anchovy, as it clearly was for *Stolephorus* (Figure 4).

Without an independent estimate of absolute abundance, there is no priori relationship between catch and P_c. This relationship must therefore be established by seeking the best possible fit between theory and observations. Speed-frequency values were plotted on tracing paper, using the semilog coordinate system of Figure 3. The resulting graph was placed over the upper panel of Figure 3 and moved up and down until a good fit resulted (right-left motion is not allowed, since the position of points along this axis is determined by size, the size-speed relationship, and net speed). This procedure is equivalent to making various assumptions about N_0, the fictitious population density at zero length, for which $P_c = 1$ by definition since $u_e = 0$. When this is done, the speed-frequency curves become speed - P_c curves, showing probability of capture for each class interval. Best fits were obtained for the 1-m net anchovy catches with $N_0 = 75$ anchovy per 100 ml wet plankton (left panel, Figure 5). For the IKMT, the best fit yielded $N_0 = 60$ anchovy per 100 ml wet plankton (right panel, Figure 5). It might have been worthwhile to treat day and night catches separately, as was done for the two types of gear, but the resulting differences in N_0 between day and night tows are small, change sign for the two different nets, and probably are not significant.

Figure 5 shows that the variance for anchovy data was smaller than that for *Stolephorus* catches (Figure 4), so that the anchovy data fit the theoretical curves somewhat better. There is no way to tell whether this difference in variance is due to differences in sampling or population structure. For both nets, day-night differences in x_0/R are small, but reaction distances tend to be slightly greater for tows taken during the day, as might be expected. A surprising result is the similarity in values of x_0/R obtained for the two nets: about 6.6 for the 1-m net and 5.4 for the IKMT (if slightly lower values for the largest size classes are ignored). This yields reaction distances, x_0, of 3.3 m for the 1-m net and 8.2 m for the IKMT. Clearly anchovy reacted to the IKMT at considerably greater distances. A light dashed line on Figure 5 (right panel) shows the dramatically increased catches which would be expected if anchovy had reacted to the IKMT at 3.3 m ($x_0/R \simeq 2$), as they apparently did in the case of the 1-m net.

The analysis shows that maximum values of P_c for the IKMT amounted to only 0.25, as compared to maximum values of P_c for the 1-m net of 0.40 or more.

Mesh retention appeared to differ for the two nets, despite similarity in mesh size (according to Murphy and Clutter, 1972, the IKMT was meshed with Nitex,[2] and the 1-m net with gauze silk, 56xxx grit, having openings of 0.505 and 0.55 mm, respectively). Retention dropped below 100%, based on deviations from the the-

[2] Reference to commercial products does not imply endorsement by the National Marine Fisheries Service.

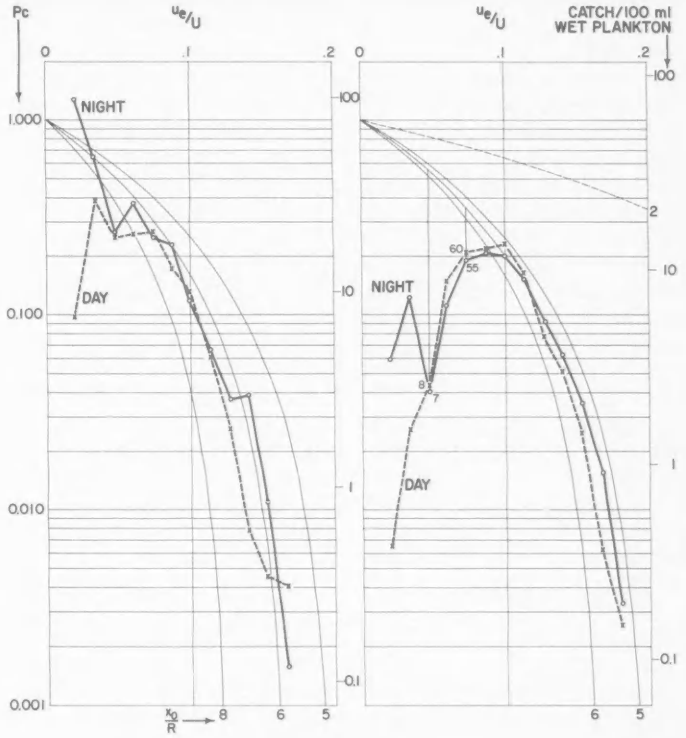

FIGURE 5.—Day and night catches of larval anchovy by a 1-m net (left) and an Isaacs-Kidd midwater trawl (right). Length-frequency data have been converted to relative escape speed (abscissa) versus frequency (ordinate, right hand scales), and compared with theoretical curves. Catch values at $P_c = 1.0$ provide estimates of abundance for all class intervals sampled. Dashed line for P_c at $x_0/R = 2$ on Isaacs-Kidd graph shows catches which could have been expected if the anchovy's reaction distance had been equal to that for the 1-m net. Net retention, based on differences between theoretical and actual catch, is shown for two class intervals on right panel: 7% to 8% for 3.75 mm fish and 55% to 60% for 5.75 mm fish. (Class sizes ranged from 1.75 mm to 12.75 and 13.75 mm by 1 mm increments.) Data from Murphy and Clutter (1972).

oretical lines of constant x_0/R, for anchovy shorter than 7.75 mm with the IKMT and 4.75 or 5.75 mm for the 1-m net. If x_0/R for a given species remains constant for any one net towed at a single speed, extrapolation of the theoretical curve toward the origin gives an indication of expected catch for smaller size classes (assuming, of course, that changes in population density with length are negligible). This use of avoidance theory is illustrated in Figure 5, right panel, where retention is calculated at 7% to 8% for 3.75-mm fish and 55% to 60% for 5.75-mm fish. These values can be easily measured on the semilog graph; the vertical distance between the "theoretical" and the observed values is transferred to the vertical coordinate scale (e.g.,

with dividers), setting the upper point at 1.0 (100%) and reading the fraction or percentage retained at the lower point.

Let us now consider catches obtained with one type of gear at two different speeds.

Aron and Collard (1969) made carefully controlled IKMT tows at two different speed ranges, at night, using telemetering flow and depth meters to insure that the amount of water sampled was the same for all tows and that sampling was done at the desired depths. The speed of their net varied between about 1.0 and 1.7 m/sec and about 1.6 and 2.3 m/sec during the two sets of tows; I have assigned values, corresponding to modal speeds, of 1.2 and 2.0 m/sec to these tows for calculating values of u_e/U.

The assumption made thus far that $u_e = 10L$, cannot be used for the species enumerated by Aron and Collard because of their large size (up to 102 mm); escape speeds of 10 body lengths per second yield values in excess of the net's speed. Either fish that big should not have been captured, or their escape speed must be considerably less than 10 lengths per second. Accordingly, it was assumed that $u_e = 5L$ (with units of cm/sec and cm).

As was noted earlier, the effect of different choices of escape velocity to length ratios is to shift the observed points along the u_e/U axis of Figure 3, with proportional changes in resulting values of x_0/R. If a set of observed points fall precisely on the theoretical curve $x_0/R = 4$, for example, a twofold change in the assumed escape velocity results in points falling equally precisely on the curves for $x_0/R = 8$ or 2, depending on whether the escape velocities are halved or doubled. Values of P_c are not affected by the choice of velocity to length ratios.

Obviously, relative values of reaction distance, x_0, can be estimated from the present theory, but absolute values can only be determined if in addition the animal's actual escape velocities are known, preferably as a function of size. Thus, from Figure 5 we can conclude with some assurance that anchovy react to the IKMT at distances some 2.5 times as great as they do to the 1-m net. But the reaction distances themselves, 8.3 m for the IKMT and 3.3 m for the 1-m net, can only be correct if anchovy do in fact swim at an average speed of 10 body lengths per second when trying to avoid the net.

Of the species enumerated by Aron and Collard, *Bathylagus stilbius* seemed most amenable to analysis with avoidance theory, because the length-frequency curves for this species were somewhat smoother, and differed more with speed of tow, than was the case for other species. Figure 6 shows the speed-frequency curves for this species, assuming that $u_e = 5L$ and that $U = 120$ and 200 cm/sec, respectively. A fairly good fit could be obtained for P_c at $x_0/R \simeq 3.8$ for the faster tow and for part of the slower tow. For the fit shown in Figure 6, N_0, the abundance at zero length, is 1,400 animals per class interval (Aron and Collard, 1969, give catches as total numbers caught during all 34 tows made in January 1966). An alternative choice of N_0, 340 animals per class interval, produces a good fit with $x_0/R = 2.4$ for the larger animals caught by the slower tows but does not fit any of the other data. In short, there is no way to fit the length-frequency data for *B. stilbius* to the theory under the assumptions used up to now.

The assumption most likely to be violated is that population size at different lengths has negligible influence on the size-frequency curve ($N_L \simeq N_0$). This assumption when valid makes it possible to fit data from a series of length classes using a single value for N_0, as was done for anchovy (Figure 5). If N_L varied significantly with length for *B. stilbius*, only identical length classes can be compared between the two sets of tows at different speeds. Figure 7 illustrates this procedure for the 62- and 97-mm length classes, where theoretical curves for P_c at $x_0/R = 2.8$ and 1.8, respectively, fit the data for these two size classes. Values of N_0 thus obtained were 900 individuals per class interval for 62-mm fish and 26 individuals per class interval for 97-mm fish. This 35-fold difference in apparent abundance is comparable in magnitude to differences in catch rates, 285 to 8 (48-fold) for the faster tows and 57 to 1 for the slower tows. It therefore seems likely that the shape of the length-frequency curves for *B. stilbius* was determined in large part by the population structure; avoidance apparently played

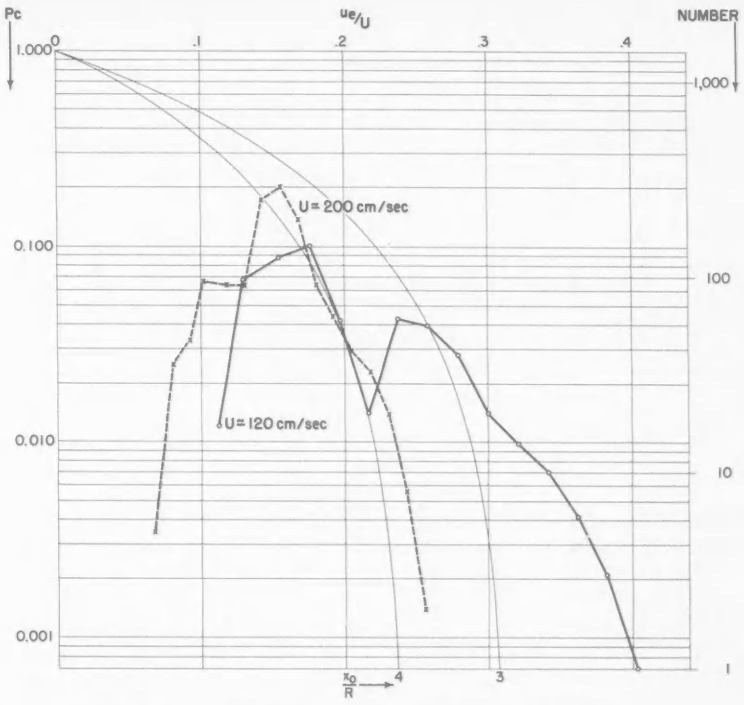

FIGURE 6.—Catches of *Bathylagus stilbius* with an Isaacs-Kidd midwater trawl at two speeds. Length frequencies converted to speed frequencies are compared with theoretical curves for P_c, showing fairly good fit at $x_0/R \simeq 3.8$ for part of data. No overall fit is possible for these observations, indicating that length-frequency curves for this species were not determined primarily by avoidance. Data from Aron and Collard (1969).

a minor role, accounting only for the difference between the 35-fold range in apparent abundance and the observed 48- to 57-fold differences in catch rates for the 62- and 97-mm size classes. The most important effect of avoidance in the *B. stilbius* catch data is the nearly constant 5-fold difference in catch rates at the two different speeds, for all animals larger than 62 mm.

Figure 7 shows sample results for only two class intervals. Table 1 shows results for all class intervals of Aron and Collard's *B. stilbius* catch data: Catches (as read from length-frequency curves), ratios of catches at two speeds, and values of x_0/R, N_0, and P_c obtained by fitting the catch data to the theoretical curves of Figure 3. Obviously, "fitting" two points to a curve is a trivial exercise, which is only justified by the apparently consistent results obtained for larger fish in Table 1. Data from three or more sets of tows, at as many different speeds, should be used for such analyses.

Figure 7 also shows the ranges of values of u_e/U, and the extreme values for x_0/R and N_0, which result when the full range of net speeds reported by Aron and Collard (1969) is used instead of the modal speeds. The numerical results, like the net speeds, vary by factors of about two—an indication of the uncertainty inherent not only in the *B. stilbius* data but also in the data for other species considered here, since variations in net speed comparable to those measured by Aron and Collard are doubtless present

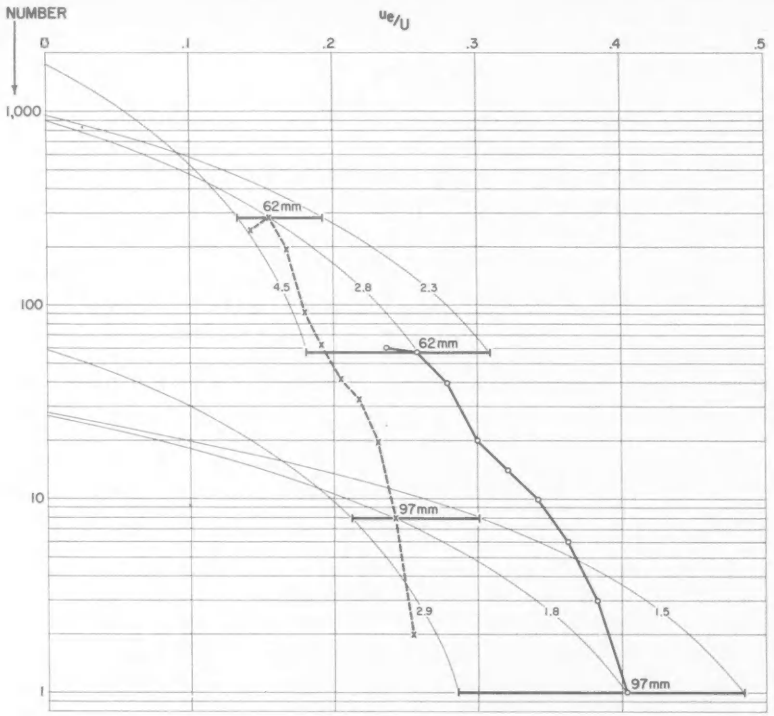

FIGURE 7.—Alternative analysis of *Bathylagus stilbius* data from Figure 6. Estimates of population (intercept of x_0/R curves for 1.8 and 2.8 with ordinate) by class interval show wide variations: from 900 animals at 62 mm to 26 animals at 97 mm. This range is comparable to the observed range in catch for these class intervals (57 to 1), showing that the length-frequency curves are primarily determined by population structure. Horizontal bars show measured ranges of towing speeds, and the effect of different speeds on the analysis. Data from Aron and Collard (1969).

during any normal towing procedure. This uncertainty does not affect the qualitative conclusions obtained from theoretical analyses; it is quite clear, for example, that anchovy react earlier to the IKMT than they do to the 1-m net. It is also quite clear that the population structure of *B. stilbius* determines the shape of the catch size-frequency curve, whereas differences in overall levels of catch for this species at two ranges of towing speed are due to avoidance, at least for those animals effectively retained by the meshes. In any case, numerical estimates of parameters such as P_c and population density which are correct to within a factor of two or less are entirely adequate for many purposes.

Simultaneous solutions for P_c as a function of length have been obtained from the theoretical equations for three pairs of samples from as many populations. The results, while not definitive, appear encouraging.

It should therefore be possible to apply the theory to a more typical set of data, a single composite sample of larval and juvenile stages of *Katsuwonus pelamis*, the skipjack tuna. These animals were sampled with a large midwater trawl, the Cobb pelagic trawl (Higgins, 1970), during a series of five equatorial cruises made by the RV *Townsend Cromwell* in 1969-70. Repli-

TABLE 1.—Analysis of catches of *Bathylagus stilbius* with an Isaacs-Kidd midwater trawl towed at two speeds, based on avoidance theory as illustrated in Figure 7. Data from Aron and Collard (1969).

Standard length (mm)	Catches		Catch ratio	Relative reaction distance x_0/R	Population abundance number per class interval	Probability of capture		Notes
	Low speed	High speed	High speed / Low speed			Low speed	High speed	
27	17	5	0.29	--	--	--	--	1
32	93	36	0.39	--	--	--	--	1
37	127	46	0.36	--	--	--	--	1
42	143	94	0.65	--	--	--	--	1
47	60	90	1.5	1.8	150	0.41	0.61	2
52	20	90	4.5	3.3	300	0.068	0.31	2
57	61	248	4.1	2.9	720	0.085	0.34	2
62	57	285	5.0	2.8	900	0.063	0.31	--
67	40	195	4.9	2.6	660	0.061	0.31	--
72	20	92	4.6	2.3	280	0.073	0.33	--
77	14	63	4.5	2.1	200	0.071	0.32	--
82	10	42	4.2	1.9	120	0.084	0.25	--
87	6	33	5.5	1.9	100	0.060	0.33	3
92	3	20	6.7	1.9	62	0.050	0.33	3
97	1	8	8.0	1.8	26	0.036	0.29	3
102	0	2	--	--	--	--	--	--

[1] Mesh losses probably significant, analysis with avoidance theory inappropriate.
[2] Mesh losses may be significant, analysis with avoidance theory questionable.
[3] Sample size inadequate, results of analysis may be seriously in error.

cate 6-hr tows were taken every night for (usually) five successive nights at each of five locations (lat 12°N, 7.5°N, 3.5°N, 0°, and 3.5°S at long 145°W) during these cruises. Catches of skipjack larvae and juveniles during each of these cruises are summarized in Table 2.

Length-frequency data from three cruises, numbers 43, 44, and 48, were kindly made available to me by Walter M. Matsumoto. These data were similar for all three cruises and were therefore pooled to obtain a smoother curve (Figure 8, right panel). Of the 510 animals in this sample, 6 could not be measured. Another 5, the largest (see Figure 8, right panel) were suspected of being atypical, possibly moribund and unable to properly avoid the trawl. Figure 8 (left panel) shows the data for the remaining animals, converted to speed frequency using $u_e = 10L$ and $U = 150$ cm/sec.

Since the skipjack population structure as a function of length, N_L, is completely unknown, two extreme assumptions are considered: First, that avoidance has no effect, so that virtually all of the drop in catch with increasing length (Figure 8) is due to changes in the population. Second, that population structure has no effect, so that the length-frequency curve is determined only by avoidance and mesh losses.

The first assumption is illustrated in Figure 9, left panel, where the lowest curve shows speed-frequency values. The straight line represents N_L, assuming the largest possible exponential decrease in population with size, consistent with the catch data. The upper curve shows P_c, obtained by dividing the catch data by N_L after setting $N_0 = 1.0$, exactly as was done on Figure 4. This analysis results in a wide range of values for P_c and x_0/R. N_0 in this case becomes 100%, equivalent to 500 individuals per class interval. Figure 9, right panel, shows P_c plotted on the linear theoretical graph of Figure 3.

The alternative extreme, assuming that $N_L = N_0$ so that population has no influence on catch length frequencies, is illustrated in Figure 10. There is no single apparent "best fit," between observation and theory, so three alternatives are considered. The upper curves, marked A, show

TABLE 2.—Skipjack larvae and juveniles caught with the Cobb pelagic trawl during RV *Townsend Cromwell* equatorial cruise series. Samples were taken along long 145°W, at lat 12°N, 7.5°N, 3.5°N, 0°, and 3.5°S.

Cruise no.	Dates	Number of tows	Number of successful tows	Skipjack caught
43	May 7-June 2, 1969	24	16	197
44	July 6-Aug. 3, 1969	25	10	154
46	Oct. 14-Nov. 13, 1969	27	11	297
47	Jan. 20-Feb. 25, 1970	21	1	1
48	Mar. 30-Apr. 30, 1970	25	15	158

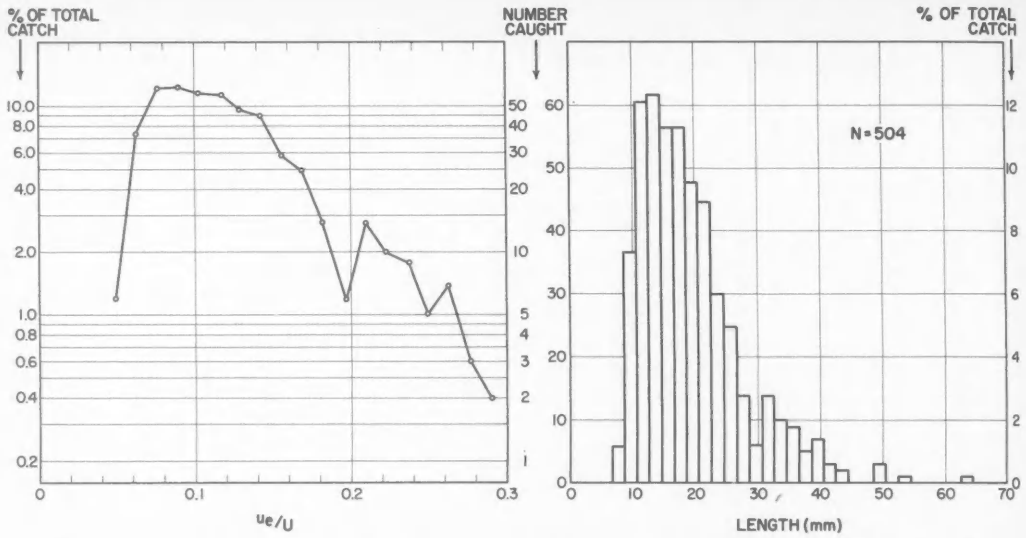

FIGURE 8.—Speed-frequency curve for skipjack larvae caught by a Cobb pelagic trawl (left panel) obtained from a length-frequency curve (right panel). Data courtesy of W. M. Matsumoto, NMFS, Southwest Fisheries Center, Honolulu Laboratory.

the data aligned to yield a fit for the best sampled class intervals. The lower curve, C, is aligned so as to fit the theoretical curves in regions of maximum slope, where sampling is most sensitive to avoidance. The middle curve, B, is a compromise which yields a reasonable fit at intermediate class intervals. Although all three analyses look plausible in the left panel of Figure 10, the linear graph shown on the right of Figure 10 clearly demonstrates that curve B yields the best match between theory and observation.

In principle there is no reason to prefer the analyses shown on Figure 10 to their alternative, Figure 9. However, I personally regard curve B on Figure 10 as the best solution because it provides the simplest and most informative explanation for the observations.

Note that all three sets of curves on Figure 10 fit two separate theoretical curves, in two distinct and well-separated groups of class intervals. As in previous examples, P_c for the largest animals markedly exceeds the values which would be expected if the theoretical x_0/R curve for smaller animals were simply extrapolated toward the right (except for curve A). In the cases of *Stolephorus* and anchovy, these anomalies were relatively minor and could reasonably be attributed to selective sampling of animals with subnormal avoidance ability. In the case of skipjack, however, this anomaly is more pronounced.

A more likely explanation for the two-part curves of Figure 10 is the construction of the Cobb trawl, which is lined with netting of two different mesh sizes: 19 mm stretched mesh of 9-thread (210 denier) nylon netting in the forward sections, with 6.4 mm stretched mesh 6-thread (210 denier) nylon netting at the cod end (Higgins, 1970). This 3-fold difference in mesh size corresponds with a nearly 3-fold difference in the size of skipjack which makes up the two components of the catch (100% apparent mesh retention at lengths greater than 15.5 mm and 37.5 mm, respectively, from curve B of Figure 10). The Cobb trawl is, in effect, two distinct nets which happen to be rigged in tandem. The openings of the trawl and its cod end during a tow are estimated to have radii of about 4 m and 1.5 m, respectively, so that their mouth areas differ by a factor of seven. The volume of water filtered by the cod end should thus

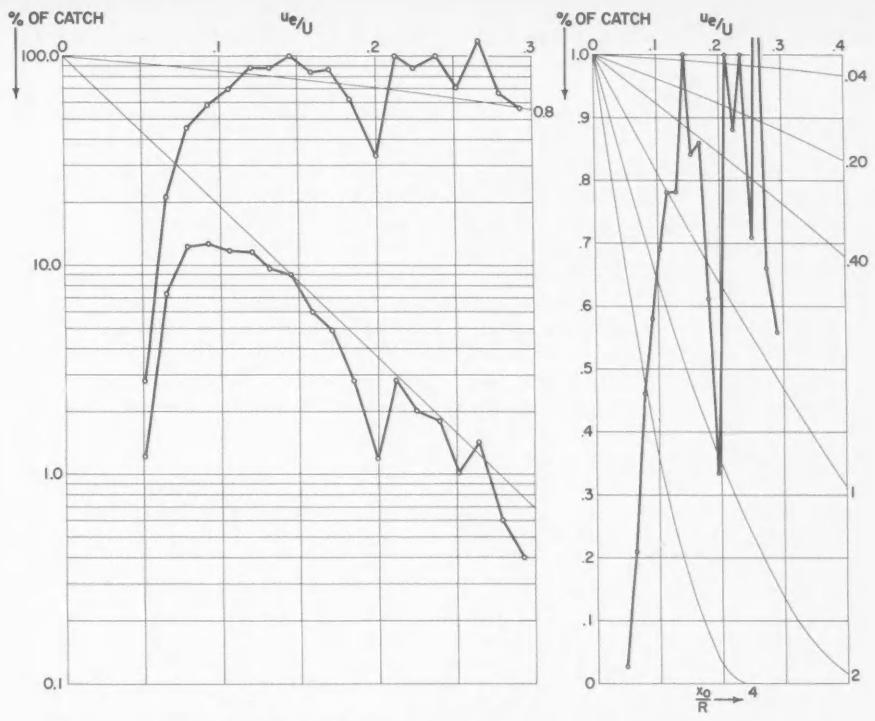

FIGURE 9.—One possible analysis of skipjack catch data, Figure 8, assuming that the length-frequency curve is determined by population density. Left panel: Lower curve, speed-frequency data, Figure 8. The straight line represents a hypothetical population density curve. Upper line shows P_c obtained by correcting catches for population changes. Right panel: Values of P_c from left panel, plotted on linear coordinates.

be somewhat less than one-seventh of the volume sampled by the trawl, because of the increased resistance to flow of the finer mesh. Catches of the six largest class intervals of skipjack all exceed the "expected" catch (theoretical curve for $x_0/R = 4$) by factors of seven or more, as would be expected if in fact these larger fish were captured by the main body of the trawl, rather than by the cod end.

The evidence suggests that curve B on Figure 10 represents a reasonable analysis of skipjack catches with the Cobb trawl. This implies that avoidance and mesh losses are dominant factors determining the size-frequency curves (Figure 8). The largest skipjack, 31.5 to 43.5 mm in length, were captured by the main body of the Cobb trawl, with P_c values between 0.05 and 0.009. Their reaction distance, x_0, was $3R$, or some 12 m. Some losses through the coarse mesh are apparent for animals smaller than 39.5 mm in length. Skipjack smaller than 31.5 mm in length were captured by the cod end of the trawl, at P_c values ranging from about 0.3 to 0.03, corresponding to reaction distances of $4R$, or 6 m. Some losses through the finer mesh are apparent for animals smaller than 17.5 mm; estimated mesh losses reach 96% for animals 7.5 mm in length. As was pointed out earlier, the above estimates of reaction distances are dependent on the assumed escape speeds, 10 body lengths per second. If the animals move faster than this, x_0 values will diminish proportionately, and vice versa.

Estimates of Pc are not affected by escape

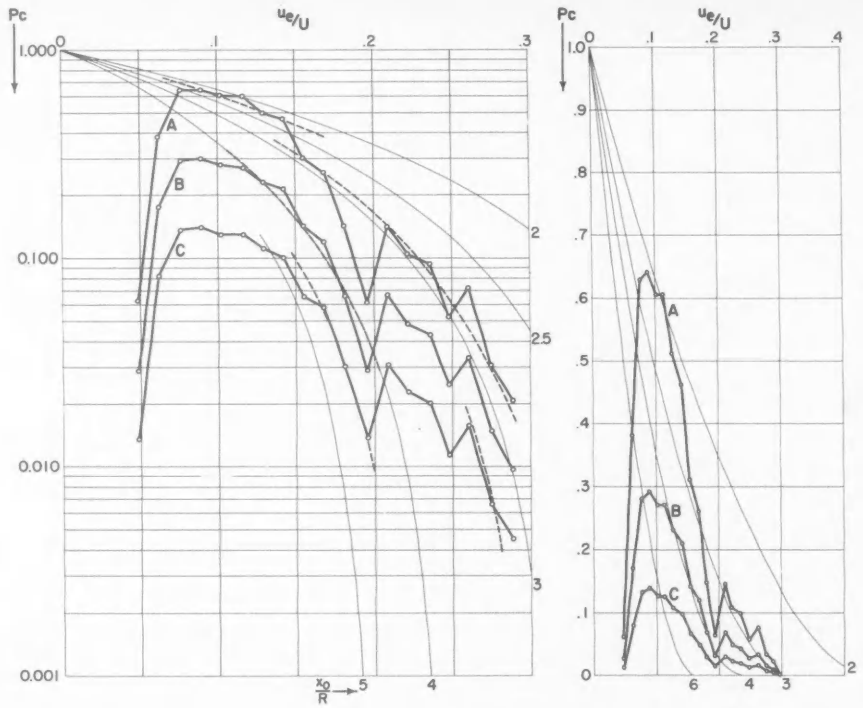

FIGURE 10.—Alternative analysis of skipjack data from Figure 8, assuming constant population density. Left panel: Three possible choices of fit between catch data and theoretical curves of P_c at constant x_0/R. Curve A shows fit for best sampled class intervals. Curve B shows fit for midrange class intervals. Curve C shows fit for regions of maximum slope. Right panel: P_c curves from left panel, plotted on linear coordinates.

speed assumptions, so the analysis yields usable estimates of population abundance of skipjack larvae and juveniles between 17.5 and 43.5 mm in length, if population structure is not important. From curve B of Figure 10, N_0 is 40% (of 499) or 200 individuals per class interval, as can be seen by placing the "% of catch" scale of Figure 9 in the proper position on Figure 10. Since abundance apparently does not seriously affect the length-frequency curve, each of the 19 class intervals sampled must also represent a population of about 200 individuals. Thus the sample of 510 skipjack was taken from a population of about 3,800, an overall catch efficiency of 13%. The total catch resulted from 41 effective tows (out of 74), an average catch per effective tow of 12.3. Accordingly, the population sampled by the Cobb trawl must have numbered roughly 94 skipjack per effective tow, to yield the observed catches at 13% efficiency. By far the greatest number of skipjack were caught by the cod end of the trawl, so the volume effectively sampled was not more than 230,000 m³ (100% filtering efficiency). This leads to an estimated mean population density for larval and juvenile skipjack of one fish per 2,500 m³, in areas where skipjack were present during the three *Townsend Cromwell* equatorial cruises.

Since P_c is by definition a minimum probability of capture, reference to equation (3) shows that the above estimate of mean population density (during a tow) represents a maximum value. On the other hand, of course, the skipjack probably were not randomly distributed, so that

a 6-hr tow doubtless underestimates their actual (as opposed to mean) population density by integrating over a 33-km distance.

Finally, two of the four species discussed here were sampled in a manner which permits use of equation (8) to estimate values of K (the product x_0u_e). Anchovy were sampled with two different nets at one speed of tow, and *B. stilbius* were sampled with one net at two ranges of speed. Table 3 shows values of K calculated for these two species. For any one choice of speeds, values of K for *B. stilbius* are nearly constant within the class intervals where fish were retained by the mesh and caught in numbers large enough to yield useful estimates of C_1/C_2, the ratio of catches obtained at the two speeds. Values of K for anchovy, on the other hand, were not constant. The latter result is not surprising, since widely different values of x_0 were obtained for the 1-m net and the IKMT whereas u_e would not be expected to differ for the two nets. Accordingly, the product of x_0u_e should not be the same for both nets, which violates the basic assumption used in calculating K with equation (8).

When values of K from Table 3 are used to calculate P_c from equation (7), the results agree with those obtained graphically for *B. stilbius* at the modal speeds, but not for anchovy. Apparently the calculated values of K for anchovy in Table 3 are too low, since they yield values of P_c which are too high, corresponding to values expected for reaction distances of about 2 to 3 m for both nets. Until avoidance behavior is better understood, equation (8) should be used with caution.

SUMMARY AND CONCLUSIONS

The ideal sampler for plankton and nekton is one whose selective characteristics are known to be appropriate, qualitatively and quantitatively, for the problem under study. Major factors determining the selectivity of towed-net samplers are avoidance and mesh selection, both of which are strongly dependent on species, size or stage of development, and physical condition. Thus the theory of towed-net selectivity must be based on a combination of general principles and detailed knowledge of the physical characteristics and behavior of each species of interest, and of each net design as well.

This preliminary study deals with one aspect of selectivity: the basic principles of avoidance. A theoretical equation is derived for P_c, the minimum probability of capture, for animals which respond individually to an oncoming sampler by attempting to dodge. The theory is based on the amount of time animals allow themselves for avoiding the net, the animal's speed relative to the net, and the geometry of the encounter. Animals are characterized by their reaction distance, x_0, and their escape speed, u_e. The net is characterized by the radius of its mouth opening, R, and its speed through the water, U. Equations (5) and (6) show the theoretical relationships between these variables and P_c; Figure 3 illustrates these equations graphically.

TABLE 3.—Values of the product $x_0u_e = K$ for anchovy and *Bathylagus stilbius*, from equation (8). Anchovy data obtained with two nets towed at one speed, day and night. *B. stilbius* data obtained with one net towed at two speed ranges; K calculated using minimum, modal, and maximum speeds for each range.

Anchovy					*Bathylagus stilbius*				
Length (mm)	Catch ratios (1-m/IKMT)		K (cm²/sec)		Length (mm)	Catch ratios (slow/fast)	K (cm²/sec)		
	Day	Night	Day	Night			Minimum speeds	Modal speeds	Maximum speeds
7.75	0.735	0.764	758	665	47	0.667	5,600	6,500	11,800
8.75	0.492	0.565	1,470	1,240	52	0.222	11,200	13,300	20,700
9.75	0.431	0.524	1,850	1,360	57	0.244	11,000	13,000	20,300
10.75	0.209	0.827	2,410	488	62	0.200	11,500	13,600	21,100
11.75	0.242	0.417	2,280	1,690	67	0.204	11,500	13,500	21,000
12.75	0.847	0.133	435	2,710	72	0.218	11,300	13,300	20,800
					77	0.222	11,200	13,300	20,700
					82	0.238	11,100	13,000	20,400
					87	0.182	11,700	13,900	21,400
					92	0.149	12,100	14,400	21,900

Testing of the theory requires some knowledge of a species' escape speed as a function of size or stage of development and its reaction distance for one or more net designs under various circumstances, so that particular groups of animals in a sample can be associated with the proper values of x_0 and u_e in the theory. If the theory is known to be valid in a given instance, x_0 can be determined once u_e is known.

The theory was evaluated against four selected sets of catch data. Since not enough was known about the swimming ability of the species in question, assumptions had to be made about swimming speed as a function of size for each one. Aside from the major premise used in deriving the theory, that animals which can escape will do so, other assumptions made in carrying out analyses of catch data were: that reaction distance is essentially constant for any one species under a given set of circumstances (one net, towed at one speed, at one time of day) and that the size-frequency curve for a species is determined entirely by mesh losses, avoidance, and the population structure—the number of animals in each size class interval in the population.

The theory was first applied to daytime catches of *Stolephorus purpureus* with a 1-m net. Simultaneous measurements made with a plankton purse seine provided information on the population structure. This nearly ideal set of data permits direct calculation of the sampling efficiency of the 1-m net, so that an absolute test of the present theory could be made. First, the bias due to population structure was removed, by dividing the catch in each class interval by the population in that class interval; this procedure also converts the catch into values of P_c for fish large enough to be completely retained by the meshes, as equation (3) demonstrates. The adjusted catch curve (the solid line labeled C_L/N_L in Figure 4) can be directly compared with theoretical curves from Figure 3 (showing P_c for various values of relative reaction distance, x_0/R), when the length class intervals have been converted to speed class intervals by assuming that the fish swim 10 body lengths per second. Agreement between theory and observation appears to be good, with some exceptions. These may be due to sampling variance, population variance, or failure of one or more assumptions used in matching *S. purpureus* to the theoretical parameters. In the latter case, the anomalies could be accounted for by incompetent avoidance behavior and school response instead of individual reaction to the net.

In the second example, the theory was used to evaluate catches of anchovy by two different nets, a 1-m net and an IKMT, towed at the same nominal speeds. Since population abundance was not determined for anchovy, an additional assumption had to be made: that the catch length-frequency curves were determined primarily by avoidance and mesh losses, as in the case of Hawaiian anchovy, where catches decrease 1,000-fold while the population decreases only by a factor of 10 in the same size interval. With this assumption, catch speed-frequency curves must also be curves of relative P_c as a function of size, or speed. Fitting the observed values to the theoretical P_c curves (Figure 5) yields a unique value for population density in each class interval, numerically equal to the catch at $P_c = 1.0$. For the anchovy, population densities of 75 and 60 animals per 100 ml wet plankton were obtained for the two samples analyzed by this method. In this case agreement between theory and observation, and between samples, seems excellent. Except for night tows with the 1-m net, values of P_c do not exceed 0.40 for the 1-m net and 0.12 for the IKMT. The only significant deviations from theory occur at smaller class intervals, where mesh losses are important. Mesh retention can be estimated quantitatively by extrapolating the theoretical curve toward smaller class intervals, for comparison with observed catches, as illustrated on the right-hand panel of Figure 5.

The third example makes use of length-frequency data for *Bathylagus stilbius* caught with an IKMT towed at two different ranges of speed. In this case, no satisfactory fit could be achieved for all larger class sizes of both sets of tows, when treated as a unit. If instead the analysis is performed using only one class interval at a time from the two sets of tows, as shown in Figure 7 and Table 1, the cause of the difficulty becomes clear. The estimated population densities have almost as great a range as do the

catches. Therefore the length-frequency curves are primarily determined by population structure, not avoidance. However, avoidance does account for the fact that faster tows caught nearly five times as many fish. Table 1 shows that P_c remained essentially constant for each set of tows over a wide range of class intervals, with values of about 0.3 for the fast tows and 0.07 for the slower ones.

The final example illustrates the use of avoidance theory for analysis of a more typical set of catch data: larvae and juveniles of the skipjack tuna caught with one net towed at one speed. The simplest way to account for the skipjack data is to assume that avoidance was more important than population structure (Figure 10). The Cobb pelagic trawl used to sample skipjack had two sizes of mesh, differing by a factor of three; the smaller mesh was used to line the cod end of the Cobb trawl. Catches of skipjack with this net fall into two groups differing in size by a factor of about three, suggesting that this trawl acts as two nets fishing in tandem. The large mesh forward end catches the largest fish, with a maximum P_c of the order of 0.03. The cod end catches smaller fish, with maximum P_c values of about 0.3. Fish of intermediate size are able to dodge the cod end but some 10% to 50% of these fish (depending on size) were retained by the larger meshes.

Analysis of four test cases leads to the conclusion that the elementary avoidance theory developed here does in fact provide reasonable interpretations of some samples obtained with towed nets. The theory's major virtue is its ability to provide relatively unambiguous estimates of probability of capture and thus of animal abundance in nature, which are not dependent on the accuracy of assumptions about swimming speeds or reaction distances. Even when the theory fails to account for observed features of the catch, it provides useful insight into the reasons for such failure and some indication of their magnitude. This is most clearly evident for losses through the mesh, but failures of the theory, or of the assumptions used in applying it, are also responsible for evidence uncovered here of incompetent avoidance behavior by smaller animals, effects of schooling on avoidance success, and the fact that avoidance has only a minor effect on the length frequencies of *B. stilbius* samples. Given our present lack of knowledge of the behavior of animals when confronted by towed samplers, it might even be said that anyone using this theory should be most cautious in precisely those cases where the theory apparently works best. A case in point is the analysis of anchovy data presented on Figure 5. Agreement between observations and theory is relatively good in this case, so that it might be easy to forget that the slope of both curves, and the apparently valid estimates of reaction distance obtained from their slopes, depend entirely on the assumed relationship between the anchovy's length and its swimming speed. Similarly, Figure 7 shows the errors which can result from assuming that the speed of the net is constant. The best contribution to the study of plankton and nekton which the present theory could make is to stimulate further research which will make the theory obsolete.

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SWIMMING AND FEEDING BEHAVIOR OF LARVAL ANCHOVY *ENGRAULIS MORDAX*

JOHN R. HUNTER[1]

ABSTRACT

The swimming and feeding behavior of laboratory-reared larval anchovy, *Engraulis mordax*, was described over the first 30 days of larval life. Estimates were made of cruising speed, proportion of time spent in rest, and burst speeds. Tail beat frequency, tail beat amplitude, and speed of swimming larvae were measured from cine photographs and the relationship between these variables determined. Complete and incomplete feeding sequences were described in detail from cine photographs and the frequency of feeding acts determined from visual observation. The extent of the reactive perceptive field for prey was measured from cine photographs and expressed as a function of larval length. Feeding success of larvae fed rotifers was determined for the first 21 days of larval life. These estimates were combined to estimate the volume of water searched by larvae per hour, and this estimate and others were used to calculate the density of food required by larvae to meet metabolic requirements. These calculations indicated that the density of food required by larvae just after yolk absorption was up to 37 times that required by older larvae.

In this report I describe the feeding and swimming behavior of the larval anchovy, *Engraulis mordax*, during the first 30 days of larval life. These observations will be combined with results of other studies in a model for estimation of the survival of larval anchovy in the sea. Similar studies of feeding and locomotor behavior have been made on other larval fishes (Blaxter, 1966; Braum, 1967; Rosenthal and Hempel, 1970), and the biology of larval fishes in general has been reviewed by Blaxter (1969).

APPARATUS AND METHODS

Anchovy larvae were reared from the egg using techniques described by Lasker, Feder, Theilacker, and May (1970). The larvae were kept in 500-liter black, fiber glass tanks in non-circulated sea water at 17° to 18°C. They were illuminated by fluorescent lamps and were given a daily dark period of 10 hr with a half hour of dim light preceding and following the dark period. Larvae were fed a variety of organisms ranging from wild plankton to laboratory-cultured brine shrimp, *Artemia salina*, the dinoflagellate, *Gymnodinium splendens*, the rotifer *Brachionus plicatilis*, and the veligers of various species of mollusks (Lasker et al., 1970; Theilacker and McMaster, 1971).

Most of the data in this report will be concerned with larvae younger than 30 days and 15 mm or less in length because larvae in this size range are more easily cultured than older ones. Metamorphosis of *Engraulis* occurs after about 50 to 60 days at 17° to 18°C when the larva is about 40 mm total length.

Visual observations of the feeding and swimming behavior of larvae were made in the 500-liter rearing tanks throughout the 13-hr day. A larva was chosen and all behavioral acts recorded continuously for 5 or more min. Behavioral acts were given a digital code, and the occurrence, duration of acts, and elapsed time were recorded on eight-channel paper tape by operation of a keyboard. The keyboard controlled a motorized paper-tape punch, and the perforated paper tape was computer-processed. Usually hundreds to thousands of larvae were present; thus a different larva was probably observed during each 5-min observation period and consequently each period was treated as an independent set of observations. A total of 447

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sets of observations was made of larvae ranging in age from 0 to 36 days.

Swimming and feeding behaviors were also recorded on motion picture film for subsequent analysis. For cine photography the larvae were placed in round plastic containers 1 cm deep and 8 to 25 cm diameter which had black opaque walls and a transparent bottom. The tank was illuminated from above by a reflector flood lamp operated below rated voltage. A water bath was inserted between the lamp and the tank to prevent heating the water. Light from the lamp was focused with a fresnel lens on the lens of the motion picture camera beneath the tank. The camera arrangement and lighting system was similar to the one used by Baylor (1959) for photographing transparent organisms with infrared radiation. From the position of the camera the subject was silhouetted against an intensely bright background because the light was focused directly on the camera lens. Thus, low sensitivity, high resolution, and high contrast film could be used. Swimming and feeding larval anchovy were photographed with a high-speed camera at 128 fps (frames per second) using AHU microfile film manufactured by the Eastman Kodak Company.[2] Photographic analysis of feeding was restricted to larvae that fed on food particles 100 μ or larger in diameter because I was not able to resolve smaller food particles and still maintain the larvae in a reasonably large photographic environment. Much slower camera speeds—1 to 2 fps—were used to estimate swimming activity.

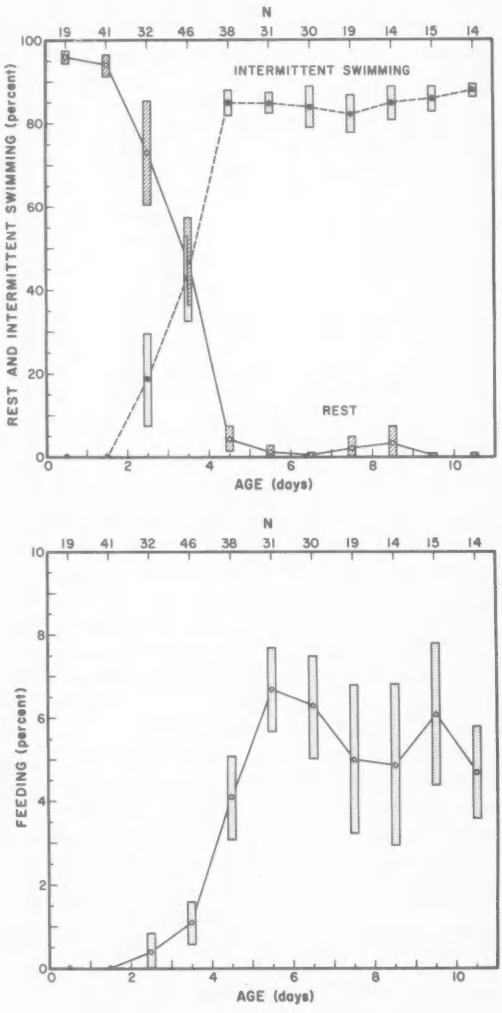

FIGURE 1.—Proportion of time spent in rest and intermittent swimming (top panel), and feeding (bottom panel) by anchovy larvae during the first 10 days of larval life. Points are mean percent $\pm$ 2 $\times$ SE, for each day; the number of observations (N) is given at top of graphs.

SWIMMING BEHAVIOR

CHANGES IN THE TYPE OF SWIMMING WITH DEVELOPMENT

During the first 2 days of larval existence, anchovy larvae exhibited little locomotor activity. Over 90% of the time they floated motionless in the water (Figure 1). Usually the head was directed downward and often the motionless yolk-sac larvae were transported slowly by water currents. Occasionally, they executed a brief but intense burst of swimming. These bursts of swimming, which I called continuous swimming, occurred about once a minute and lasted

[2] Use of trade names does not imply endorsement by the National Marine Fisheries Service.

1 to 2 sec (Table 1). During a burst the tail and body beat continuously from side to side without interruption, and the larva accelerated and decelerated rapidly. Bursts of continuous swimming usually occurred in the absence of any observed stimulus although some bursts were stimulated by accidental contact with other larvae or the walls of the tank.

During the third day of larval life (age 2 days) a new swimming pattern appeared which was to become the dominant mode of locomotion throughout the rest of larval existence. The new mode of swimming was intermittent swimming, consisting of alternate periods of swimming and gliding; typically the larva executed one full tail beat, paused, and glided forward without beating the tail and then repeated the sequence of beating and gliding. The mean proportion of time devoted to intermittent swimming increased during the third and fourth days of larval life, more or less in proportion to the decrease in the time spent in rest (Figure 2). By the fifth day of larval life about 85% of the observation period was composed of intermittent swimming whereas the proportion of time devoted to rest during the day was nearly zero.

With the appearance of intermittent swimming the frequency and duration of continuous swimming decreased. Bursts of continuous swimming occurred once or twice per minute during the first 2 days of larval life whereas by the tenth day they occurred only once in 5 min, and the duration of the bursts also declined over the same period (Table 1). Bursts of continuous swimming occurred at a low frequency throughout the rest of larval life.

TABLE 1.—Proportion of observation time spent in continuous swimming and the mean duration, and mean frequency, of bursts of continuous swimming during the first 10 days of anchovy larval life.

Age days	Percent of observation time Mean ± 2 × SE	Frequency of bursts/min Mean ± 2 × SE	Duration of bursts (sec) Mean ± 2 × SE	N
0	2.4 ± 0.86	0.85 ± 0.28	1.86 ± 0.50	20
1	5.2 ± 0.99	1.72 ± 0.32	1.72 ± 0.48	32
2	2.0 ± 0.58	1.38 ± 0.22	1.38 ± 0.52	28
3	3.4 ± 0.24	0.76 ± 0.78	0.76 ± 0.22	45
4	0.7 ± 0.10	0.33 ± 0.06	0.33 ± 0.16	37
5	0.12 ± 0.16	0.11 ± 0.12	0.37 ± 0.54	32
6	0.16 ± 0.12	0.10 ± 0.22	0.31 ± 0.22	27
7	0.22 ± 0.16	0.18 ± 0.06	0.41 ± 0.26	11
8	0.15 ± 0.18	0.13 ± 0.12	0.23 ± 0.24	13
9	0.29 ± 0.20	0.29 ± 0.18	0.30 ± 0.16	15
10	0.10 ± 0.08	0.20 ± 0.08	0.22 ± 0.14	14

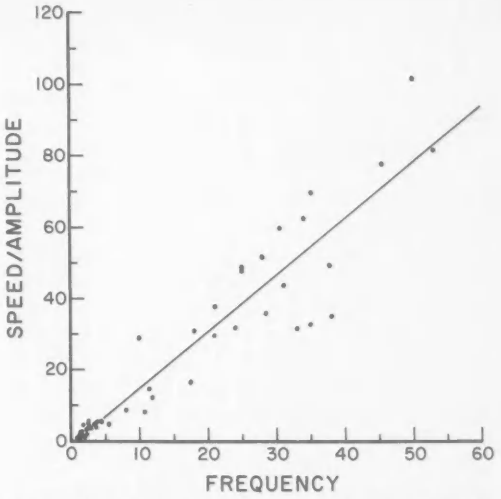

FIGURE 2.—Relationship between speed, tail beat frequency, and tail beat amplitude for anchovy larvae for all types of swimming. Equation for line is $V/A = -1.11 + 1.59\ F$ where V/A is speed (cm/sec) divided by tail beat amplitude (cm), and F is tail beat frequency (beats/sec).

The appearance of intermittent swimming coincided with the appearance of feeding behavior. Feeding behavior was closely associated with intermittent swimming; food was sighted during intermittent swimming and the larvae advanced on the prey using this mode of lomocotion.

POSSIBLE SIGNIFICANCE OE SPONTANEOUS BURSTS OF SWIMMING IN YOLK-SAC LARVAE

The regularity of the bursts of continuous swimming of yolk-sac larvae (age 0-1 day) suggests that the bursts may have a respiratory function. Yolk-sac larvae have no functional gill filaments, and oxygen must be obtained through the integument. Thus the regular bursts of continuous swimming could be necessary for gas exchange. I conducted a short experiment to test this hypothesis.

I measured the duration and frequency of bursts of swimming of age 0 day and 1 day larvae in open 10-liter containers containing water

saturated with oxygen and in ones containing water below saturation at 17°C. In the tests below saturation the initial level was 30% of saturation, but it increased to 65% by the end of the observation period 7 hr later.

At oxygen concentrations below saturation, larvae of both ages swam more frequently than did the controls of the same age ($P \leqslant 0.008$ Mann Whitney U Test, Siegel, 1956). Age 0 day larvae spent 5.36 ± 1.41% (± 2 × SE, N = 15) of the time swimming in water below saturation whereas they spent 1.97 ± 0.64% (N = 10) of the time swimming at saturation. Age 1 day larvae spent 12.48 ± 4.50% (N = 5) of the time swimming in water below saturation whereas the controls spent 3.30 ± 2.31% (N = 5). The proportion of time spent swimming by the controls in both tests did not differ from that given in Table 1 for larvae of the same age.

This experiment suggests that the regular bursts of swimming of yolk-sac anchovy larvae have a respiratory function. On the other hand, the increase in swimming could have been the result of stress induced by low oxygen concentrations and bear no relationship to behavior under normal conditions. I am not inclined to accept this explanation because except for the increase in the duration and frequency of swimming, the behavior of the larvae was normal. A different motor pattern, vigorous shaking of the head, appears at lethal or near lethal levels of oxygen, about 12% of saturation at 17°C.

STRUCTURE OF CONTINUOUS AND INTERMITTENT SWIMMING

To estimate the relationship between larval anchovy tail movement, size, and speed during continuous and intermittent swimming, 53 film sequences were analyzed frame by frame. They included sequences of artificially stimulated and spontaneous bursts of continuous swimming and of bouts of intermittent swimming. In each swimming sequence the mean tail beat amplitude, swimming speed, and tail beat frequency were measured by use of a coordinate reader and digitizer (Hunter and Zweifel, 1971). I assumed that the net course swam was equivalent to a path formed from the midpoints of the tail beat. If the course was straight, this estimate was the same as a regression of the X and Y coordinates for the positions occupied by the head or about the same as a straight line fit by eye through frame by frame tracings of the larva. If the course was curved, the path formed by the midpoints provided a reasonable estimate of the net curvilinear path followed by the larva.

Typically intermittent swimming could be separated from continuous swimming at a glance, but when the tail beat frequency approached that of continuous swimming it was difficult to distinguish between the two types of swimming. Thus, to separate all data into one of the two classes of swimming it was necessary to determine the beat frequency at which larvae changed from intermittent to continuous swimming. This was accomplished by measuring the elapsed time between beats in the slower swimming sequences.

When the tail was beat at a frequency of 4.7 beats/sec or higher, the movement of the tail was continuous, that is, the interval of rest between beats was equal to or less than 0.0078 sec (1 frame at 128 fps). At tail beat frequencies at or below 4.4 beats/sec the movement of the tail was not continuous but rather pauses of 0.086 to 0.811 sec existed between beats. The mean of the duration of rest between beats was 0.30 ± 0.22 sec (±2 × SE) whereas the duration of a single beat was 0.13 ± 0.05 sec. The duration of the pause or glide between beats was independent of larval size or swimming characteristics and was quite variable. The speed of tail movement was also independent of size but was about the same in all larvae. Thus, at beat frequencies below 4 beats/sec, larvae decreased speed by increasing the interval between beats but maintained about the same speed of tail movement.

Continuous and intermittent swimming data (Table 2) were analyzed separately to determine the relationship between tail beat amplitude, speed, length, and tail beat frequency. The general equation $V/A = a + bF$, where A is amplitude in cm, F is tail beat frequency, V is speed in cm/sec, and s_t is the standard deviation about the line, provided the best fit to continuous and intermittent data sets. The intercepts and slopes

for the two data sets were nearly the same, and consequently I combined the data and obtained the relationship of $V/A = -1.11 + 1.59F, s_t = 8.311$ for all data (Figure 2).

The principal difference between the above equation and ones derived by Bainbridge (1958) or by Hunter and Zweifel (1971) for adult fishes was that amplitude was the estimator of size instead of length. Amplitude was required in the present study because during bursts of continuous swimming larvae modulated the amplitude of their tail beat. Inclusion of length in addition to amplitude and frequency did not improve the relationship. In the study by Hunter and Zweifel (1971) fish did not modulate the amplitude of the tail beat because they swam at a steady speed. Amplitude is known to change during acceleration (Gray, 1968), and the behavior of larvae during bursts of continuous swimming was no exception to this rule.

During intermittent swimming, amplitude was not modulated but was maintained at a minimum value of about one-fifth of a body length. The relationship between amplitude and length during intermittent swimming was obtained by the equation $A = 0.112 + 0.170\ L$ where $s_t = 0.066$ (Figure 3).

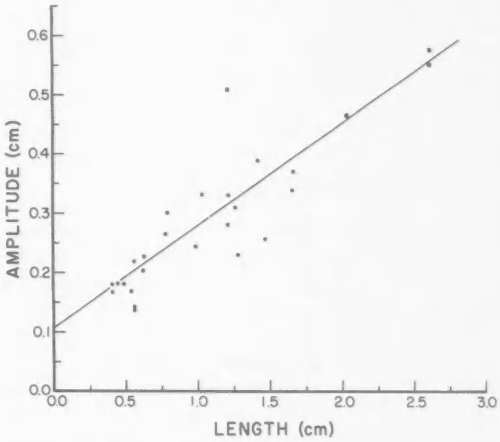

FIGURE 3.—Relationship between anchovy larval length (cm) and tail beat amplitude (cm) for intermittent swimming.

TABLE 2.—The speed, tail beat frequency, and tail beat amplitude for anchovy larvae of various lengths during continuous and intermittent swimming. Each value is a mean for a single swimming sequence swum by one larva.

Continuous swimming				Intermittent swimming			
Length	Speed	Tail beat frequency	Tail beat amplitude	Length	Speed	Tail beat frequency	Tail beat amplitude
cm	*cm/sec*	*beats/sec*	*cm*	*cm*	*cm/sec*	*beats/sec*	*cm*
0.34	4.71	38.1	0.133	0.41	0.31	2.3	0.169
0.37	4.59	33.3	0.142	0.41	0.30	2.0	0.182
0.38	0.75	5.5	0.143	0.45	0.33	2.4	0.183
0.39	10.68	45.5	0.137	0.49	0.20	2.3	0.181
0.41	1.22	10.9	0.150	0.54	0.64	3.8	0.170
0.42	1.08	4.7	0.194	0.56	0.44	2.1	0.221
0.42	8.05	35.3	0.115	0.57	0.73	4.5	0.138
0.42	11.63	50.0	0.114	0.57	0.37	2.7	0.142
0.42	3.86	17.9	0.124	0.62	0.17	1.1	0.205
0.43	7.28	30.5	0.121	0.63	1.01	2.8	0.229
0.43	8.92	34.5	0.140	0.78	0.63	1.3	0.267
0.43	7.91	28.2	0.152	0.79	0.52	1.5	0.302
0.43	7.48	38.5	0.147	0.98	0.20	1.4	0.245
0.44	12.18	53.3	0.148	1.03	1.61	3.1	0.333
0.44	4.89	35.3	0.148	1.21	1.23	2.8	0.514
0.50	9.61	24.7	0.200	1.21	1.35	2.3	0.278
0.56	2.52	17.5	0.150	1.21	1.52	2.6	0.332
0.72	1.75	8.0	0.206	1.27	1.18	2.7	0.310
0.72	2.17	11.4	0.150	1.28	1.27	2.6	0.231
0.93	4.28	10.2	0.148	1.42	1.02	2.1	0.390
1.00	11.22	28.6	0.311	1.47	1.26	3.2	0.257
1.00	15.91	20.7	0.422	1.66	1.02	1.7	0.340
1.24	31.26	31.6	0.716	1.66	0.78	1.7	0.372
1.24	9.08	12.0	0.718	2.04	1.68	2.2	0.468
1.24	23.16	21.0	0.777	2.62	2.50	1.9	0.581
1.32	21.16	24.0	0.664	2.62	3.02	2.9	0.555
1.42	26.85	25.0	0.545				

At intermittent swimming speeds tail movement was slow enough that the frequency of the beat could be counted by eye. If the length of the larva were known, intermittent swimming speed could be estimated from the general speed equation given above, the amplitude equation for intermittent speeds, and the tail beat frequency. Instead of the general speed equation it may be preferable to use one based on intermittent swimming data alone, which is $V/A = 0.0466 + 1.308\ F$ where $s_l = 1.160$.

BURST SPEEDS

The speeds obtained by larval anchovy during bursts of fast continuous swimming are of interest because they may be a measure of the larva's ability to avoid predators or possibly plankton nets. Bursts of fast swimming were stimulated in larvae of mean length 4.1 ± 0.1 mm (Table 2, continuous swimming, 0.34 to 0.44 cm larvae) and mean length 12.1 ± 1.2 mm (Table 2, continuous swimming, 1.00 to 1.42 cm). Bursts were stimulated by moving a pin near a larva and photographing the larva at the film speed of 200 fps. Speeds were averaged for the entire duration of the burst, which lasted about 0.1 to 0.2 sec. The stimulated burst speed for larvae of mean length 4.1 mm was 63 ± 19 mm/sec (mean ± 2 × SE) or about 15 body lengths/sec and that for the 12.1-mm larvae was 198 ± mm/sec or about 16 body lengths/sec. The maximum speed obtained by larvae in the 4.1 mm length class was swum by a 4.2-mm larva which swam 116 mm/sec (28 body lengths/sec) during a burst of 0.12 sec. The maximum speed for larvae in the 12.1 mm class was 313 mm/sec (25 body lengths/sec) swum by a 12.4-mm larva during a burst lasting 0.10 sec. In summary, larvae had a maximum speed capability of 25 body lengths/sec or faster for bursts lasting 0.1 to 0.2 sec, but the typical or average burst speeds were close to 15 body lengths/sec.

ESTIMATES OF DAILY RATE OF SWIMMING

I shall consider only intermittent swimming in the estimates of daily swimming rate because only intermittent swimming was associated with food search, and because once feeding began, continuous swimming was an insignificant proportion of daily activity (Figure 1 and Table 1). Two independent methods were used to estimate the rate of intermittent swimming. In the first method, larvae were photographed at 2 fps in a cylindrical chamber of 25 cm diameter, and swimming speed calculated from frame-by-frame analysis of the photographs. Five minutes of swimming were analyzed for each larva; swimming was divided into intermittent and continuous types; and periods of inactivity equal to or greater than 5 sec were tabulated as rest. In the second method, visual observations of larvae in the 500-liter rearing tanks were used to record the tail beat frequency of larvae during intermittent swimming and the frequency and duration of continuous swimming and rest. Larvae were observed three or more times a day. The speed of larvae during intermittent swimming was calculated from the tail beat frequency by use of the relationships between age, length, amplitude, tail beat frequency, and speed previously described.

The speed of intermittent swimming measured from photographs increased with larval length (Figure 4), and the regression of speed on length gave the relationship $V = -0.215 + 1.038\ L$ where $s_l = 0.280$. Visual measurements of tail beat frequency of intermittent swimming

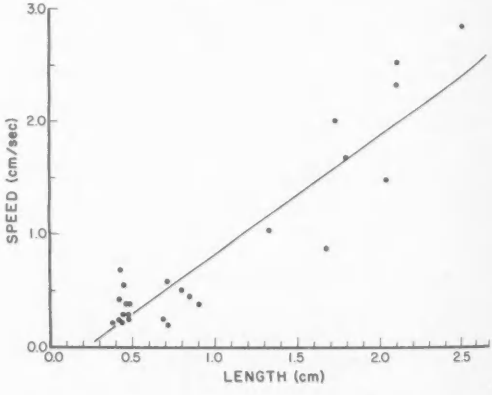

FIGURE 4.—Rate of movement during intermittent swimming (cm/sec) as a function of anchovy larval length (cm). Measurements taken from analysis of cine photographs. Equation for line is $V = -0.215 + 1.038L$.

TABLE 3.—Comparison of visual and photographic estimates of speed of intermittent swimming for anchovy larvae of three sizes.

Larval length (cm)	Tail beat amplitude[1] (cm)	Intermittent speed estimates (cm/sec)		Distance traveled[4] (m/hr)	
		Visual[2]	Photographic[3]	Visual	Photographic
0.5	0.197	0.414	0.304	12.3	9.0
1.0	0.282	0.592	0.823	17.6	24.5
1.5	0.367	0.771	1.342	22.9	39.9

[1] Estimated from $A = 0.112 + 0.170L$.
[2] Estimated from $V/A = 0.047 + 1.308F$, where $F = 1.57$.
[3] Estimated from $V = -0.215 + 1.038L$.
[4] When 82.6% time spent swimming.

did not change with age over the first 30 days of larval life. That tail beat frequency did not change implied that the interval of rest between beats, the principal determinant of frequency, was dependent on variables unrelated to size or development. The same conclusion was obtained from analysis of the structure of intermittent swimming in the preceding section. Thus, the change in speed associated with increased length or age may be a function of only the increase in tail beat amplitude with length.

The mean tail beat frequency for intermittent swimming, 1.57 ± 0.03 beats/sec, was substituted into the speed equation for intermittent swimming. Speed of intermittent swimming could then be determined for larvae of any length by substitution of the appropriate tail beat amplitude into the equation. Speed estimates in which the above procedure was used and ones based on photographic analysis are compared in Table 3. The two sets of estimates are reasonably close for 0.5-cm larvae but they diverge for larger ones. No reason exists to disregard either set of estimates. It seems reasonable to assume that the true values lie somewhere between them.

The proportion of daylight hours devoted to intermittent swimming must be considered to estimate the distance traveled per hour. Visual observations are preferable for this purpose because of the greater number of observations (318) and because visual observations were systematically taken at different times of day. Between ages 4 and 30 days, no trend with age existed in the proportion of time devoted to swimming although time spent swimming decreased slightly on days of intensive feeding. The mean proportion of time devoted to intermittent swimming was 82.6 ± 1.2%. To arrive at this estimate I considered periods of inactivity longer than 5 sec as rest and periods equal to or less than 5 sec as a part of intermittent swimming bouts. Estimates of the distance traveled per hour, assuming 82.6% of the time is spent swimming, are shown in Table 3. These values will be combined with others to estimate rate of food search in a later section.

FEEDING BEHAVIOR

DESCRIPTION OF FEEDING BEHAVIOR

After a larva sighted a prey, the head turned toward it so that the prey was perpendicular to the tip of the snout and thus in about the center of the binocular field of the larva. Then, while keeping the prey in the center of the binocular field, the larva swam slowly toward the prey by executing one or more tail beats. After swimming ceased, the larva contracted its body into an S-shaped striking posture typical of the larval clupeoid fishes (Figure 5). During contraction of the body, the prey was maintained directly in front of the snout and small movements by the prey were compensated for by slight adjustments in the orientation of the head and larger movements by rotating the entire body with the pectoral fins. The larva continuously moved toward the prey while forming the strike posture by high frequency (50 to 60 beats/sec), low amplitude vibration of the finfold or caudal fin.

The order and rate at which portions of the body were contracted to form the S-strike posture were not fixed. The order appeared to be related to the initial orientation of the head and trunk. Frequently swimming movements were integrated into the beginning of the strike posture. The larva while approaching a prey often ceased swimming with the body partially bent, and the contractions to form the strike posture were carried onward from that point. Variations in the rate of contraction were related to movements of the prey. If the larva did not keep up with a moving prey, contraction of the body was often interrupted and the incomplete posture held for an extended period. The ampli-

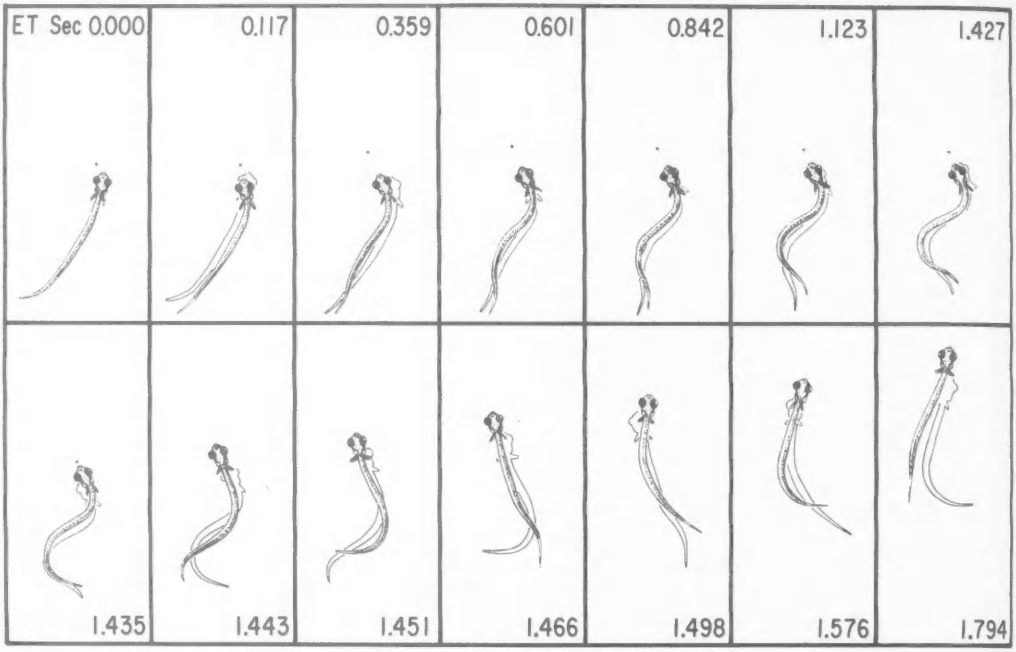

FIGURE 5.—Tracings of selected motion picture frames from a feeding sequence of an anchovy larva (8.9 mm, 21 days old) and a prey taken at 128 frames per second. Frame lines are fixed such that distance moved by larva is indicated by comparison of tracings; and unshaded image indicates position of larva in the preceding tracing. The following events are illustrated: elapsed time (ET) 0 sec, larva sights prey; ET 0-0.117 sec, larva orients head toward prey and swims toward it; ET 0.117-1.435 sec, larva forms *s*-shaped strike posture; ET 1.435-1.443 sec, strike begins and prey captured; and ET 1.451-1.794 sec, forward movement continues as tail returns to axis of progression.

tude of the posterior bend in the body reached a maximum just before the strike was begun.

The larva began the strike by drawing the tip of the tail rapidly anteriorly. It then thrust the tail backward, extended the head, opened the mouth, and the particle was taken or missed within 7.8 to 15.6 msec after the beginning of the backward thrust of the tail (one to two frames at 128 fps). The entire feeding sequence from sighting the prey to the strike lasted only 1 to 2 sec. The sequence of movements were so rapid that my first impression was that they were extremely stereotyped. Later, frame-by-frame analysis of film taken at 128 fps indicated that normal variance was associated with every characteristic that could be measured in the films.

Larvae of 15 to 20 mm formed the strike posture in less time than did one 5 to 15 mm long, and consequently, feeding sequences were shorter in larger larvae (Figure 6). On the other hand, the time used to approach the prey before forming the strike posture was about 0.6 sec in larvae of all sizes. Other characteristics increased directly in proportion to length, for example, the maximum amplitude of the body in the strike posture, the distance to the prey at the time of the strike, and the rate of movement toward the prey while in the strike posture. The speed of the strike also increased with length but the relationship appears to be nonlinear. The speed of the strike relative to length was less in the largest size class of larvae.

INCOMPLETE FEEDING SEQUENCES

Feeding sequences often ended before they were completed by execution of the strike. The mean frequency of feeding strikes (the last act in the feeding sequence) for all visual observations for larvae of ages 4 to 27 days was 1.28 ± 0.14 strikes/min (N = 325) whereas that for the orientation movement of the head (the first act in the sequence) was 3.22 ± 0.30. Thus, about 40% of all feeding sequences were completed. The proportion of feeding sequences that were completed did not change with age, but there was some indication that the proportion of incomplete sequences increased when the larvae began to feed on *Artemia* nauplii. This increase in the proportion of incomplete sequences was caused by an increase in the proportion of sequences ended at the first act, the orientation movement of the head. The proportion of feeding sequences that were carried as far as bending the body was 52% and remained about the same regardless of age or food type.

In the film analysis I analyzed only incomplete feeding sequences that were continued beyond the head orientation movement and compared them with completed sequences. These measurements indicated that some feeding sequences ended at every stage up to and including the final strike posture, and the duration of incomplete sequences overlapped that of completed ones (Table 4). The only characteristic measured in the photographs that consistently separated incomplete from completed feeding sequences was that at the end of incompleted ones the prey was farther away from the larvae than it was in completed sequences. Thus, the principal cause of the failure to continue a feeding sequence was an inability to closely approach the prey while forming the strike posture.

To summarize, photographic analysis of incomplete and complete feeding sequences indi-

TABLE 4.—Comparison of characteristics of incomplete and complete feeding sequences for larval anchovy 5.1-10.0 mm.

Characteristic	Incomplete sequence[1] Mean ± 2 × SE	Complete sequence[2] Mean ± 2 × SE
Duration of S-posture (sec)	0.82 ± 0.26	1.11 ± 0.16
Duration entire sequence (sec)	1.38 ± 0.40	1.71 ± 0.26
Body amplitude (mm)	1.03 ± 0.40	1.52 ± 0.20
Distance to prey at end of sequence (mm)	0.81 ± 0.17	0.41 ± 0.04
S-posture forward movement (mm/sec)	0.51 ± 0.26	0.80 ± 0.34

[1] N = 19.
[2] N = 13.

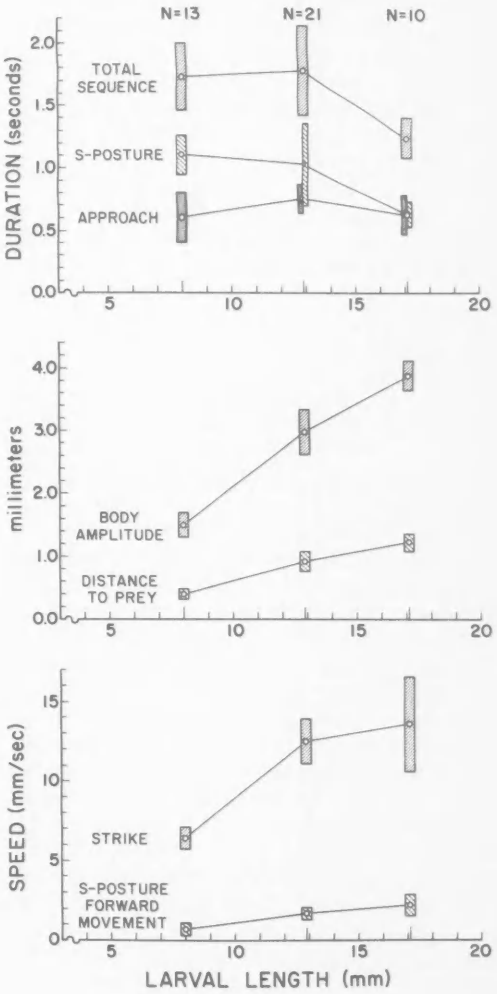

FIGURE 6.—Characteristics of complete feeding sequences of anchovy larvae taken from film analysis. Values are means ± 2 × SE for three size classes of larvae (5.1-10.0, 10.1-15.0, and 15.1-20.0) and are plotted at the mean length of the larvae in the class.

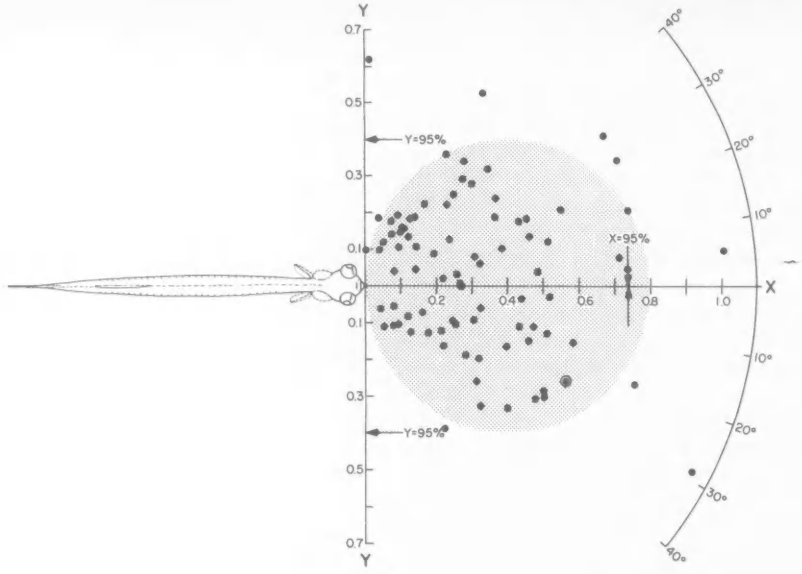

FIGURE 7.—Reactive perceptive field in the horizontal plane for anchovy larvae. Each point represents position of a prey in the horizontal plane at time larvae first reacted to it. Distances in X and Y axes were divided by the lengths of the larvae and expressed as proportions of larval length. Arrows indicate lines that would enclose 95% of prey sighted in each plane.

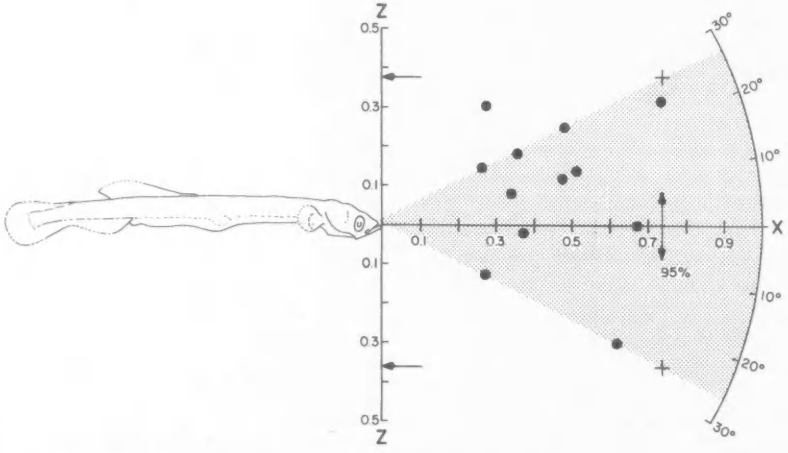

FIGURE 8.—Reactive perceptive field in the vertical plane for anchovy larvae. Distances on X and Z are expressed as a proportion of larvae length; points are position of prey when larvae first reacted to them; crosses indicate point of intersection of visual cone with $Y = 95\%$ (the 95% limit of prey distribution in Y given in Figure 7); and arrows on Z indicate projected values of Z for intersection points.

cated that considerable flexibility exists in what appeared to be a highly stereotyped feeding pattern. Although a sequence was completed in only 1 to 2 sec, the larvae depend on feedback from the prey throughout the period. The larvae respond to the prey during the sequence by adjusting posture, speed, and direction of movement and by ending or continuing the sequence.

EXTENT OF REACTIVE PERCEPTIVE FIELD

The size of the predator's reactive perceptive field (Holling, 1965) is an essential element in the estimation of the rate of search for prey by a predator, that is, the extent of the area in which a predator will react to a prey. In studies on larval fishes the cross-sectional area of the perceptual field is multiplied by the speed of swimming to estimate the volume of water searched per unit of time. Estimates of this type have been made by Braum (1967), Rosenthal and Hempel (1970), and Blaxter (1966) and are summarized by Blaxter (1969).

To determine the position of prey when larvae first reacted to them feeding, larvae were filmed from below for horizontal measurements and separately from the side for measurements in the vertical plane. Seventy-one horizontal film sequences of larvae, 4.0 to 24.2-mm, and 12 vertical sequences of larvae, 7.0 to 24.7 mm, were analyzed frame by frame.

In the film analysis all measurements were made in reference to the body of the larvae; X signified measurements made in the axis of progression or swimming plane; Y those in the other horizontal axis; and Z those made along the vertical axis. Vertical measurements were made in relation to the orientation of the larvae and were not necessarily vertical in relation to the water surface. Searching behavior was independent of body orientation. Larvae reacted to prey when they swam upward, when they swam downward, as well as when they swam parallel to the water surface.

In each photographic sequence the angle and distance of the prey from the tip of the snout of the larva were measured 15 msec before the larva reacted to the prey by turning the head toward it (two frames at 128 fps). To correct for obvious length-dependent differences in field size the distance to the prey was divided by larval length and was expressed in body lengths (L). Prey organisms included *Brachionus*, various veliger larvae, *Artemia* nauplii, and wild copepod nauplii of undetermined species.

In the horizontal plane larvae reacted only to prey ahead of them; prey at 90° or more from the tip of the snout were not selected, and most prey were less than 60° from the snout (Figure 7). The reactive perceptive field in horizontal cross section was roughly circular. A circle of radius $0.4L$ with the center on the axis of progression or X axis enclosed 90% of all prey sighted (shaded area, Figure 7). In the vertical plane, larvae reacted to prey below as well as above the X axis. The maximum distance above and below the X axis at which prey were sighted in the vertical plane was $0.3L$ and thus the maximum extent of Z was $0.6L$ (Figure 8). The reactive perceptive field may be roughly triangular in vertical cross section, because a triangle with a central angle of 53° and altitude of $0.74L$ enclosed all but one of the 12 observed values.

Maxima seem appropriate rather than averages to estimate the extent of the reactive perceptive field because only the exceptional larva survives in nature and because field size may change with feeding motivation. Considering the two axes in the horizontal plane separately, for 95% of all prey sighted the value Y for the position of prey was equal to or less than $0.4L$ from the axis of progression (X axis), and for 95% of all prey the X values for prey position were equal to or less than $0.74L$. Ninety-five percent limits could not be used to estimate Z because the observations were too few to calculate percentages. The maximum observed Z value above and below the X axis was $0.3L$. This value could be used or alternatively Z could be estimated at a point on X by assuming the field is triangular in cross section as illustrated in Figure 8. Using the 95% limit for X, $0.74L$, as the point to make the cross section, we obtain an estimate of $Z = 0.36L$. Thus, the estimate of the maximum extent of Z varied from 0.30 to $0.36L$ depending on the assumptions used. Assuming an elliptical cross section where $Y = 0.40L$ and $Z = 0.36L$ the area of the ellipse is

equal to $0.45L^2$ for a cross section at $X = 0.74L$. To estimate the volume search per unit time these areas need to be multiplied by the larval swimming speed. This aspect of the calculation will be considered in a subsequent section.

FEEDING RATES

In all studies in this paper larvae were observed and maintained in tanks containing high and presumably optimum food densities (*Gymnodinium* 100 to 200/ml, *Brachionus* 10 to 20/ml, and *Artemia* nauplii 3 to 10/ml). It is unlikely that density limited the rate of feeding under these conditions. Thus, the rates recorded probably are near the maximum feeding rate that can be sustained by larval anchovy.

Records were kept of the frequency of feeding acts of larvae ages 4 to 27 days raised in the 500-liter rearing tanks. A total of 325 observations of 5-min duration was taken at three different times of day. No trend in the frequency of feeding strikes with time of day existed. The larvae fed actively throughout the day although their guts were filled after the first half hour of feeding each morning. The average frequency of feeding strikes for all data combined was 1.28 ± 0.144 strikes/min. Some evidence existed that the rate may climb to 3 strikes/min for 2 to 3 days when *Artemia* nauplii were first introduced, but no direct cause and effect relationship could be established because other prey were also present in the tank.

Another estimate of feeding rate was obtained from the data on feeding success described in the next section. The larvae in that study had empty guts at the beginning of the observation period, and they were observed during their initial 10 min of feeding on a particular day, whereas the preceding data observations were begun about a half an hour after the larvae began feeding and continued throughout the day. The average feeding frequency for larvae studied in the feeding success experiments ($N = 100$) was 1.75 ± 0.205 strikes/min and the range was from 0.2 to 5.8 strikes/min. Thus, during the first 10 min of feeding, feeding rates were on the average somewhat higher than they were when averaged over the entire day. Feeding rates on *Artemia* were the same as those on *Brachionus*.

FEEDING SUCCESS

Feeding success was estimated by counting the number of feeding acts completed in 10 min, removing the larvae from the container, and counting the number of prey in the gut. Larvae were kept in the dark for 12 or more hr before the test to insure that the gut was empty (anchovy larvae do not feed in the dark). I measured the feeding success of larvae fed *Brachionus* (density, 10 to 60/ml) from the first day of feeding (age 3 to 4 days) up to the 21st day of larval life. A separate experiment was run to determine the effect of a different prey on feeding success. At age 17 days the diets of some of the larvae were changed from one of only *Brachionus* to one of *Artemia* nauplii (density, 3 to 15/ml). Measurements of feeding success were made over the first week of feeding on *Artemia*. *Gymnodinium* was not used as a food for first feeding larvae because it was usually defecated before we were able to examine the contents of the gut. Two measurements of feeding success of larvae fed *Gymnodinium* fell within the scatter for *Brachionus* (Figure 9).

The success of larvae fed *Brachionus* rapidly increased over the first week of feeding (age 3 to 10 days), but thereafter the rate of increase of feeding success was much lower. The form of the relationship between age and success was that of a learning curve. A semilog transformation of the data provided an adequate correction for this curvilinear trend. The regression of feeding success in percent on the log of larval age gave the relationship, percent success = 93.2 (log age) — 33.30 where $s_l = 20.14$.

Seventeen-day-old larvae were less successful in capturing *Artemia* for the first time than they had been in capturing *Brachionus*. Only 37% of feeding acts were successful when larvae were fed *Artemia* nauplii for the first time at age 17 days whereas 81% were successful when the food was *Brachionus* (Figure 10). The initial level of feeding success for larvae fed *Artemia* was higher than that of larvae when they first began to feed at age 3 to 4 days, and less time was required to obtain a high level of success on *Artemia* than was required for first feeding larvae. By the third day of feeding on *Artemia*

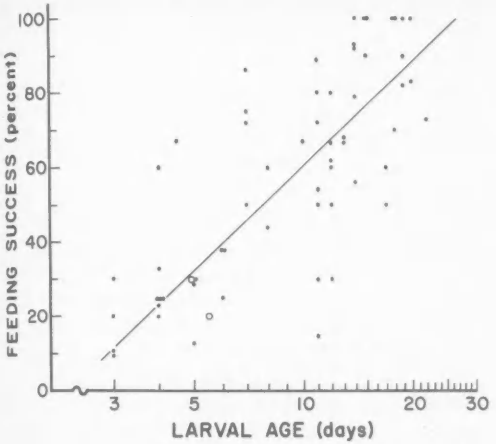

FIGURE 9.—Feeding success (percent of prey captured) of anchovy larvae of various ages fed *Brachionus*. Larval age is plotted on log scale, equation for line is percent success = 93.2(log age) − 33.30. Two open circles, larvae fed *Gymnodinium*.

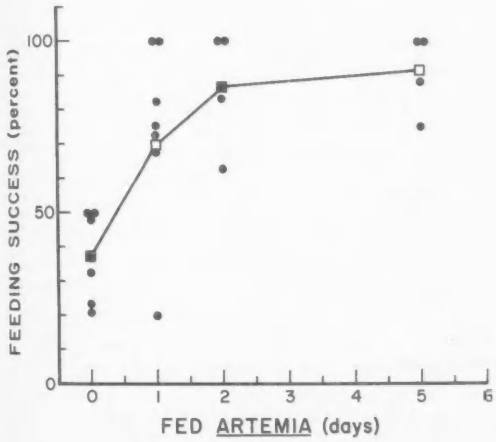

FIGURE 10.—Feeding success of anchovy larvae fed *Artemia* for the first time at age 17 days (0 days on abscissa) and for 5 additional days. The line connects mean values.

the level of success had reached the same level as it had after 2 weeks of feeding on *Brachionus*.

One interpretation of these results is that a considerable proportion of feeding experience on one type of prey is transferable when larvae feed on a new prey. On the other hand, the surprisingly long period (about 2 weeks) required to achieve a high level of feeding success on *Brachionus* suggests that maturation of sensory and locomotor systems may also play a role in anchovy larval feeding behavior during the first 2 weeks of larval life.

ESTIMATION OF VOLUME SEARCHED

In this section I combine the estimates made in the previous section to estimate the volume of water searched by larvae per hour and will use this estimate and others in a subsequent section to calculate the density of food required by larvae to meet metabolic requirements.

The volume of water searched per hour by larvae was calculated by multiplying the cross-sectional area of the reactive perceptive field by the distance traveled per hour by larvae. I made separate calculations for the photographic and the visual speed estimates given in Table 3. In both calculations the speed estimates were adjusted for the proportion of time spent swimming, 82.6%, and they were extended from distance/sec to distance/hr. In this and all subsequent calculations I have made larval age and length interchangeable by using the growth equation $l_t = 3.24e^{0.0555t}$ given by Kramer and Zweifel (1970) who reared anchovy larvae at 17°C under conditions similar to those used in this study.

The estimate of the volume of water searched per hour increased exponentially with size (Figure 11). The two volume estimates were close for larvae less than 10 mm long but they diverged for larger ones. There was no reason to select one estimate over the other and, consequently, I chose to use the average of the two for future calculations. When the two estimates are averaged the outcome is nearly the same as the relationship, volume searched/hr = $1{,}000L^3$, where L is larval length in cm and volume is in cm^3, or simply, liters searched/hr = L^3. Examination of Figure 11 shows the line for L^3 falls almost midway between the two estimates. I shall use the average estimate in the rest of the calculations, but L^3 could be used with only a negligible difference. In the larger larvae L^3

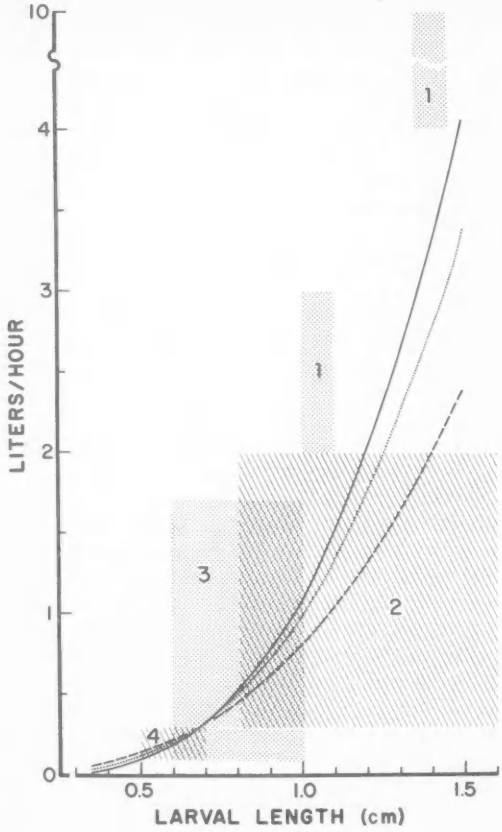

FIGURE 11.—Estimates of liters/hour searched by anchovy larvae 0.3-1.3 cm total length. Lines are based on average estimates and are not data points. Solid line is the volume searched when the photographic estimate of swimming activity was used; dashed line, the volume searched when visual estimate of swimming activity was used; and dotted line, the relationship, liters/hour = L^3, where L is total larval length (cm). Rectangles enclose estimates of search rates for other larval fishes from the literature: 1) *Clupea* (Rosenthal and Hempel, 1970); 2) *Clupea* (Blaxter, 1969); 3) *Pleuronectes* (Blaxter, 1969); and 4) *Sardina* (Blaxter, 1969).

yields a slightly higher estimate than the average estimate, but the difference does not exceed 5% even in the largest larva under consideration.

That the change in volume searched with length was nearly proportional to L^3 could be expected. The volume is the product of the speed and cross-sectional area of the perceptive field for prey. I assumed a length coefficient of one in the calculation of cross-sectional area (area = $0.45L^2$), and the length coefficients for the two swimming speed estimates were close to one as is commonly the case in swimming speed studies (Bainbridge, 1958; Hunter and Zweifel, 1971). Thus the product of the length coefficient for speed and the one for area would be expected to be close to L^3. On the other hand, that the product of the various constants used in the calculation was close to 1,000 was simply chance.

The estimates of volume searched made for other larval fishes, shown as rectangles in the figure, are close to the two for anchovy, especially when the variance in such estimates is considered. How much of the difference between anchovy and other species can be attributed to specific differences and how much to differences in technique and assumptions is unknown. For example, differences in techniques of estimation of the distance of prey at the time of sighting could account for the differences between my results and others. The initial movement of the head toward the prey was easily detected in the films, but it is possible that a significant period elapsed between recognition and movement of the head. If this is true, I have underestimated the size of the perceptive field for prey. Perhaps some of the herring estimates are higher than the anchovy because the anchovy swims more slowly. Anchovy swim more slowly because unlike most pelagic fishes the anchovy swims intermittently; that is they glide between beats of the tail.

ESTIMATION OF FOOD DENSITY

To fulfill their metabolic requirement larval anchovy must ingest about 686 rotifers/day/mg dry weight or the caloric equivalent. This estimate was derived from the following: 4.5 μliter of O_2/mg dry wt/hr is consumed by anchovy larvae kept on a 14-10 hr light-dark cycle (Lasker, personal communication); 1 μliter O_2 = 0.005 cal; caloric value of the rotifer (*Brachionus*) = 5,335 ± 139 cal/g (Theilacker and Mc-

Master, 1971); dry weight 1 rotifer = 0.16 μg of which 92.2% is organic material (Theilacker and McMaster, 1971); and the assumption of 100% digestive efficiency. The estimate was converted from unit weight to length by the length-dry weight relationship of log W = 3.3237 log L — 3.8205 given by Lasker et al. (1970).

The metabolic requirement given above was adjusted for feeding success by increasing it in proportion to the number of prey missed during feeding as predicted by the feeding success equation presented previously. The density of food required for survival was estimated by dividing the food requirement adjusted for feeding success by the volume of water searched in 10 hr. The average of the photographic and visual estimates of volume searched was used to calculate the volume searched by larvae. A 10-hr feeding period was chosen purely as a convenience because the actual duration of daily feeding periods is unknown.

The density of rotifers required to meet metabolic requirements decreased exponentially with size (Figure 12). First feeding larvae, 3 days old (3.5 mm) require 105 rotifers or the caloric equivalents/liter during a 10-hr feeding period whereas 10-day-old larvae (5.9 mm) require only 34 rotifers/liter. Older larvae require much lower food densities primarily because feeding success increases exponentially with age.

Density estimates based on rotifer equivalents probably underestimate the prey density required during the first few days of feeding because a smaller prey is needed by most anchovy larvae during this time. For example, Theilacker and McMaster (1971) found that only 12% of anchovy larvae survive to 19 days old when *Brachionus* was the only food, whereas 40 to 50% survived if in addition to *Brachionus* the dinoflagellate, *Gymnodinium*, was present during the first few days of feeding. To obtain a better estimate of food density required by larvae during the first days of feeding I estimated the caloric value of a single *Gymnodinium* cell and recalculated the density required in terms of dinoflagellate equivalents. The caloric value of a single *Gymnodinium* cell was estimated from the carbon content (Mullin and Brooks, 1970) and by assuming that the carbon content

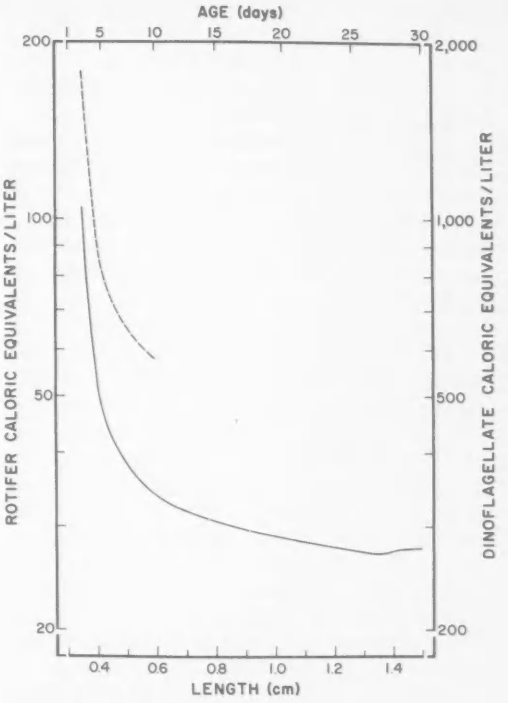

FIGURE 12.—Estimate of the density of prey in rotifer caloric equivalents/liter (left ordinate, solid line) and in dinoflagellate equivalents (right ordinate, dashed line) required to meet metabolic requirements of larval anchovy of 0.3-1.5 cm. Lines are based on average estimates. The shapes of the two curves are the same, but they differ in elevation by a constant factor of 17.

represented 40% of the organic material and that the caloric value of *Gymnodinium* was 5,000 cal/g of organic material. According to this calculation the caloric value of a single *Brachionus* is about 17 times that of a single *Gymnodinium* cell. Thus larvae feeding on dinoflagellates require about 17 times the prey density (dashed line Figure 12) than do those feeding on rotifers (solid line). Nearly all larvae are able to feed on *Brachionus* by age 5 days; thus, the food density requirement for the majority of the larvae shifts from 1,790 dinoflagellates/liter at age 3 days (the first day of feeding) to 48 rotifer equivalents/liter at age 5 days.

Although there are some differences, most of the assumptions and procedures I used were similar to those used by Rosenthal and Hempel (1970) to estimate food densities required by herring larvae. Rosenthal and Hempel estimated that the minimum food ration for herring larvae 10 to 11 mm was 4 to 8 nauplii/liter and the maximum was 21 to 42/liter. My minimum estimate based on metabolic considerations for a comparable size anchovy larvae was 29/liter. For the minimum density they assumed, as I have, that the larva struck at all prey that entered its perceptive field, but for the maximum density they assumed that only a part of the plankters perceived resulted in a completed feeding sequence. In the anchovy larvae feeding on food at high density, on the average only 40% of feeding sequences were completed. Thus, using a similar criterion for a maximum ration as Rosenthal and Hempel (1970), the maximum density required for anchovy larvae would be 2.5 times the minimum ration or for a 10- to 11-mm larva about 72 rotifer equivalents/liter. Considering specific differences and the differences in assumptions and procedures, the estimated food requirements of herring larvae by Rosenthal and Hempel (1970) do not differ much from the one calculated for an anchovy larva of comparable size.

In a survey of the literature given by Blaxter (1965) the densities of food for larval cluepoid fishes in the natural environment ranged from 1 to 68 items/liter. Arthur (1956) in a comprehensive study of the food of pelagic larvae in the California Current region found 1 or more nauplii/liter in 72% of his samples and 30 or more nauplii/liter in about 3% of his samples. Beers and Stewart (1967) measured the density of copepod and naupliar and post naupliar stages (35 to 103 μ) in a 600-mile transect in an area of anchovy abundance and obtained densities ranging from 5 to 17 copepods/liter. Thus, food in the natural environment appears to be near or below the minimum concentration I estimated was required for older larvae but considerably below that for first feeding larvae.

Nearly every adjustment that could be made in my estimates of food requirements for anchovy larvae would sharpen the differences between early and late larval stages or elevate the overall food requirement. For example, natural prey would be of greater variety and could be more difficult to capture, thus causing a differential increase in food concentration required by younger larvae. In addition, older larvae are capable of feeding on a greater variety of food because they can feed on all food used by younger stages plus larger prey as well. I assumed a digestion efficiency of 100% but it must be less than that and this would also increase the overall food requirement. In short, an adjustment in the estimates would probably increase the difference between the estimated food density requirements taken from laboratory measurements and natural food densities.

Laboratory measurements indicated that larval anchovies are more vulnerable to death from starvation just after yolk absorption than at any other time during larval life. This conclusion agrees with those drawn from similar laboratory studies on the herring and other species. Whether or not the increased vulnerability to a starvation death just after yolk absorption is related to year class strength as contended by Hjort (1914) is still a debated question (Blaxter, 1969; Saville, 1971). The catch curves for larval anchovy over 10 years give no indication of an increase in mortality just after yolk absorption (Lenarz, 1972). Three explanations for the absence in the anchovy of an early critical period are: first, turbulence may generate random movement between fish larvae and prey and thereby considerably extend the search volume (Murphy, 1961); second, it may be that the mortality of larvae at all stages is so great because of starvation and other causes that the increased vulnerability at the youngest stages is not detectable; and third, food may not be limiting for early larvae because of patchy food distribution. The absolute number of prey required by early anchovy larvae is not great but a high concentration is required; hence, the patch size could be quite small. It would be of interest in this regard to determine the size, density, and distribution of food patches in the natural environment on a scale appropriate to fish larvae. It would also be of interest to determine the

extent larvae are adapted in their searching behavior to a patchy food distribution.

SUMMARY

1. During the first 2 days of larval life (age 0-1 day) anchovy larvae spent 95% of the time resting. Rest was interrupted once a minute by a burst of continuous swimming lasting 1-2 sec. By age 4 days, yolk was completely absorbed; 85% of the time was spent in intermittent swimming, 7% in feeding, and only 4% in rest. The proportion of time spent in each of these activities remained about the same thereafter.

2. Intermittent swimming was associated with food search. It consisted of repeated sequences of a single tail beat followed by a glide. The speed of the tail was a constant; thus, tail beat frequency was a function of the glide duration. During intermittent swimming tail beat amplitude (A) was the constant proportion of length (L) expressed by the equation, $A = 0.112 + 0.170L$.

3. In continuous swimming, larvae executed a burst of swimming in which no pauses existed between tail beats. Both tail beat frequency and amplitude were modulated during the burst because the larvae accelerated and decelerated. Larvae had a burst speed capability in excess of $25L$/sec for bursts lasting 0.1-0.2 sec, but the typical or average burst speed was near $15L$/sec. The speed (V), tail beat frequency (F), and amplitude (A) relationship for continuous and intermittent swimming were expressed by the equation, $V/A = -1.11 + 1.59F$.

4. The daily rate of movement of larvae excluding rest was estimated using visual and photographic techniques. Measurements taken from cine photographs gave the relationship $V = -0.215 + 1.038L$. Visual observations indicated that average tail beat frequency during intermittent swimming was a constant for larvae of different sizes, and this value was used to provide an additional estimate of the daily rate of movement.

5. The size of the reactive perceptive field for larval anchovy was determined from cine photographs taken in vertical and horizontal planes by plotting the position of prey when larvae first reacted to them. The limits of the perceptive field were set to include 95% of the prey sighted. The field was elliptical, and increased with length and had a cross section proportional to $0.45L^2$.

6. Larvae first reacted to prey by turning the head toward the prey. The larvae then swam toward it, stopped swimming, coiled the body into an S-shape, and struck at the prey by thrusting the tail backward and extending the head. The total feeding sequence lasted only 1-2 sec. Throughout the sequence the larva adjusted its body to compensate for movements by the prey and slowly moved toward the prey by vibrating the finfold or caudal fin.

7. Only 40% of all feeding sequences were completed. Sequences were ended at all stages up to just before the strike began. The principal cause of failure to complete a feeding sequence after a larva began to form the S-shaped posture was the inability of the larva to close the distance between it and the prey.

8. Under conditions of high food density, larvae fed throughout the day. The average feeding rate for larvae 4 to 27 days old was 1.28 completed feeding sequences/min. During the initial filling of the gut in the morning the mean rate was to 1.75/min.

9. Feeding success of larvae fed *Brachionus* increased rapidly from 11% success on the first day of feeding (age 3 days) to 50% by age 8 days, but the rate of improvement was more gradual thereafter. The relationship between feeding success and age was expressed by the equation, % success = 93.2 (log age) — 33.30. Seventeen-day-old larvae were less successful in capturing *Artemia* for the first time than they had been in capturing *Brachionus*, but after 3 days of feeding experience on *Artemia* the larvae regained their former level of success.

10. The liters of water searched per hour by larval anchovy were estimated by combining the estimate of the reactive perceptive field with an estimate of sustained swimming activity. When the average of the two swimming activity estimates was used, the estimate of volume searched was nearly the same as the relationship, liters searched/hr = L^3 where L is larval length in cm.

11. The density of rotifers and dinoflagellates required for larvae to meet metabolic needs was

calculated from caloric and respiration data, and estimates of volume searched and feeding success. These calculations indicated that anchovy larvae just after yolk absorption require up to 37 times the food density as older larvae. Thus, just after yolk absorption anchovy larvae are more vulnerable to death from starvation than at any other time during the larval stage.

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MESH RETENTION OF LARVAE OF *SARDINOPS CAERULEA* AND *ENGRAULIS MORDAX* BY PLANKTON NETS

WILLIAM H. LENARZ [1]

ABSTRACT

Mesh retention of the standard plankton sampling gear used by the California Cooperative Oceanic Fisheries Investigations between 1949 and 1968 for larvae of the Pacific sardine (*Sardinops caerulea*) and northern anchovy (*Engraulis mordax*) was estimated by comparing catches made by the standard gear with a gear that retains larvae of all sizes. The results indicate that 67% of sardine larvae and 60% of anchovy larvae are retained by the meshes of the standard gear. The standard gear was replaced by a similar gear in 1969. Apparently all anchovy larvae are retained by the new gear. The new gear is the same as the old gear except for the netting. The netting of the new gear is constructed from 0.505-mm mesh width nylon while the netting of the standard gear was constructed from 0.55-mm mesh width silk. Catch curves of anchovy and sardine larvae corrected for escape through meshes revealed no evidence of a critical period.

Although fisheries literature contains numerous examples of estimates of mesh retention of fish by commercial fishing gear, there is little quantitative work on mesh retention of fish larvae by plankton gear. A review of such studies by Vannucci (1968) revealed only three papers containing quantitative estimates of mesh retention by plankton gear. The lack of knowledge on this subject can cause serious errors when comparing the estimates of abundance of fish larvae made from samples taken by different sampling gears or of two or more species of fish larvae by the same gear.

This paper presents estimates of mesh retention of larvae of the Pacific sardine (*Sardinops caerulea*) and northern anchovy (*Engraulis mordax*) by plankton nets that have been used by the CalCOFI (California Cooperative Oceanic Fisheries Investigations). Estimates are made of the errors that result because mesh retention is ignored when the relative abundance of the two species is calculated and when abundance of the anchovy is computed using data from two quite similar types of sampling gear. Finally the catch curves of the two species are examined for evidence of the critical period proposed by Hjort (1926).

Several authors have noted that small larvae of the Pacific sardine and northern anchovy are not completely retained by the meshes of the plankton nets used by the CalCOFI, but did not have the necessary data to make quantitative estimates of the retention rates. Ahlstrom (1954) noted that small sardine larvae were not fully retained by the meshes of the net in use at that time. Ahlstrom (personal communication) attempted to obtain a measure of the retention rates with a series of paired plankton samples made with a regular CalCOFI net and a net with a finer mesh, but failed to capture an adequate number of sardine larvae. Isaacs (1965) concluded that anchovies up to 7.75 mm were not fully retained by the meshes. He attributed differences in the form of catch curves of anchovy larvae in different years to changes in the minimum size of complete retention. Murphy (1966) stated that anchovy larvae are undersampled ". . . by a factor of about 2, relative to sardines, i.e., they tend to pass through the mesh of the net to a marked extent." He did not describe his method of obtaining the estimate but later informed me (Murphy, personal communication) that he based his conclusion on comparison of catch curves with hypothetical curves based on the assumption of exponential mortality. Lenarz (in press) estimated that

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northern anchovy larvae were undersampled by a factor of 3.4 relative to sardine larvae because of differences in retention rate and rate of decline in catch with increase in size. His estimates of retention rates also were based on differences between observed catch curves and hypothetical curves based on a constant rate of decline.

METHODS

The data for this study on fish larvae were taken from CalCOFI plankton tows. From 1949 to 1968, CalCOFI used a single silk net (type 1) of 0.55-mm mesh with a 1-m diameter mouth opening. During 1966-68 this net was paired with one of nylon of 0.333-mm mesh (type 2) with a ½-m diameter mouth opening. In 1969 the netting of the larger net was replaced with monofilament nylon netting of 0.505-mm (type 3). The variance of mesh width of the type 3 net is considerably less than that of the type 1 net. Other details of the net characteristics are available from Smith[2]. The nets were lowered and raised obliquely at a rate of 1.5 knots to a depth of 140 m in 1966-1968 and to 210 m during 1969. Since very few anchovy or sardine larvae occur below a depth of 140 m, the change in depth should make no difference in the results of this study. Other details of sampling are described by Ahlstrom (1966).

All sardine and anchovy larvae in each sample were identified and measured to the nearest 0.5 mm, standard length. The data revealed evidence of varying degrees of personal bias towards favoring measurements of whole millimeter rather than half millimeter. Sette (1950) was aware of the potential for this type of bias in measuring adult fish and stated: "... to avoid personal bias in favor of whole or half centimeter marks, the measuring scale had uniform graduation marks and they were serially numbered. In addition to avoiding bias, this had the advantage of giving two digit numbers for all listings and computations, the data being divided by two for conversion to centimeters at the final stage of work." Perhaps it would be prudent to follow the advice of Sette, if 0.5 mm accuracy is desired. Evidence of personal bias in measuring the smallest sizes of larvae was also noted. Since the smallest larvae are often distorted, it is difficult to make objective measurements. Because of the above described biases, measurements of the larvae are grouped into the intervals shown in Tables 1 and 2. Larvae captured by the type 2 net were multiplied by the ratio of volume of water sampled by the type 1 net to the volume of water sampled by the type 2 net to adjust for the smaller size of the type 2 net. The samples were chosen on the basis of the presence of sardine larvae or moderate numbers of anchovy larvae.

The following equations, using the notation of Regier and Robson (1966), were used to estimate mesh retention of the type 1 net

$$n_{1jk} = S_{1j}n_{2jk} + e_{jk} \qquad (1)$$

where n_{ijk} = number of larvae of size L_j caught by type i net in kth sample.

s_{ij} = mesh retention of type i net to larvae of size L_j, i.e., $s_{ij} = n_{ij}/N_j$

where N_j = either absolute or relative number of larvae of size L_j in the population.

e_{jk} = error term that is assumed to be normally distributed and independent of n_{2jk}.

The use of equation (1) to estimate mesh retention of the type 1 net implies the assumption that s_{2j} is 1 for all j, i.e., $N_j \approx n_{2j}$. Preliminary analysis of data obtained from a series of paired samples of the type 2 net and a finer meshed net indicates that this assumption is valid for northern anchovy and Pacific sardine (P. E. Smith, personal communication). This method of estimating S_{1j} from a known or estimated N_j is noted as the "direct approach" in the terminology of Regier and Robson (1966).

The least squares estimate of s_{1j} is given by Cochran (1963) as

[2] Paul E. Smith, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, Calif.

TABLE 1.—Catches of northern anchovy larvae by type 1 (0.55-mm mesh) and type 2 (0.333-mm mesh) nets for each sample.

Cruise	Station	Net type	Standard length							
			2.5	3.75	4.75	5.75	6.75	7.75	8.75	9.75
6601	93.35	1	141	175	38	18	17	14	4	0
		2	994.950	55.275	22.110	25.795	14.740	0.000	0.000	0.000
6601	103.29	1	95	121	291	145	45	23	10	5
		2	164.250	141.255	351.495	128.115	42.705	22.995	13.140	3.285
6601	120.24	1	22	51	66	62	30	21	15	4
		2	32.330	54.961	109.922	42.029	42.029	32.330	22.631	12.932
6601	120.35	1	25	59	37	17	11	0	0	0
		2	36.113	68.943	36.113	16.415	0.000	0.000	0.000	0.000
6607	113.50	1	3	1	1	1	0	0	1	0
		2	9.716	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6607	117.45	1	0	11	23	22	13	6	6	5
		2	4.448	84.512	44.480	26.688	12.344	4.448	8.896	0.000
6607	118.39	1	17	64	22	9	8	10	14	0
		2	208.518	117.858	13.599	13.599	9.066	4.533	4.533	4.533
6607	119.33	1	96	72	109	126	90	56	33	9
		2	32.508	102.168	130.032	130.032	116.100	55.728	32.508	9.288
6607	120.25	1	8	11	2	2	0	0	0	0
		2	97.196	128.122	26.508	8.836	4.418	0.000	0.000	0.000
6607	133.23	1	1	0	0	0	1	0	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6607	137.22	1	3	58	217	133	91	45	25	3
		2	8.212	143.710	316.162	176.558	90.332	86.226	36.954	16.424
6607	137.23	1	6	29	41	60	45	27	13	2
		2	66.195	61.782	105.912	52.956	26.478	30.891	8.826	13.239
6608	87.35	1	360	11	13	6	6	8	2	0
		2	877.150	162.190	122.470	33.100	39.720	26.480	6.620	3.310
6608	130.28	1	23	43	21	10	1	1	1	0
		2	29.552	51.716	18.470	0.000	0.000	0.000	0.000	0.000
6608	130.30	1	13	29	29	15	7	1	0	0
		2	47.879	66.294	22.098	11.049	11.049	7.366	0.000	0.000
6608	133.25	1	32	19	7	8	2	0	1	0
		2	151.578	79.398	21.654	25.263	7.218	0.000	0.000	0.000
6610	120.40	1	0	0	0	0	0	0	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6610	130.28	1	0	5	6	9	2	3	0	1
		2	0.000	7.128	10.692	0.000	0.000	0.000	0.000	0.000
6611	120.25	1	0	0	0	0	0	0	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6611	137.23	1	32	1	1	0	0	0	0	0
		2	127.575	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6706	83.55	1	9	17	36	53	35	33	23	25
		2	41.808	62.712	70.551	39.195	44.421	23.517	15.678	33.969
6706	110.40	1	21	6	30	57	56	52	48	58
		2	3.074	3.074	24.592	18.444	36.888	12.296	15.370	3.074
6706	120.24	1	1	0	0	4	4	1	0	0
		2	6.278	0.000	0.000	0.000	3.139	0.000	0.000	0.000
6706	120.40	1	2	4	14	31	19	26	12	7
		2	0.000	0.000	17.550	14.625	14.625	20.475	5.850	5.850
6712	107.45	1	123	106	18	10	13	1	5	0
		2	287.586	114.297	11.061	14.748	14.748	0.000	0.000	0.000
6712	120.50	1	333	23	9	11	7	6	1	0
		2	496.110	14.380	0.000	7.190	17.975	0.000	3.595	3.595

$$\tilde{s}_{1j} = \frac{\sum_{k=1}^{m} n_{1jk} n_{2jk}}{\sum_{k=1}^{m} n_{2jk}}, \qquad (2)$$

where m = number of samples.

However, if the assumption of independence of e_{jk} is violated, (2) is not the least squares estimate of s_{1j}. A form of violation of the assumption which is common in plankton sampling is that the error term is proportional to $\sqrt{n_{2jk}}$. In this case the least squares estimate of s_{1j} is given by Cochran (1963) as

TABLE 2.—Catch of Pacific sardine larvae by type 1 (0.55-mm mesh) and type 2 (0.333-mm mesh) nets for each sample.

Cruise	Station	Net type	Standard length							
			2.5	3.75	4.75	5.75	6.75	7.75	8.75	9.75
6601	93.35	1	0	0	0	0	0	0	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6601	103.29	1	0	0	0	2	1	0	0	0
		2	0.000	3.285	3.285	0.000	0.000	0.000	3.285	0.000
6601	120.24	1	1	2	7	8	4	3	0	1
		2	0.000	3.233	16.165	6.466	12.932	0.000	0.000	0.000
6601	120.35	1	0	1	38	4	0	0	0	0
		2	0.000	3.283	42.679	0.000	0.000	0.000	0.000	0.000
6607	113.50	1	0	0	2	8	0	0	0	0
		2	0.000	0.000	4.858	4.858	0.000	0.000	0.000	0.000
6607	117.45	1	0	0	0	2	8	5	5	3
		2	0.000	0.000	0.000	13.344	8.896	8.896	17.792	13.344
6607	118.39	1	0	3	16	17	4	2	0	0
		2	0.000	0.000	31.731	18.132	0.000	0.000	0.000	0.000
6607	119.33	1	0	0	0	0	2	1	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6607	120.25	1	4	3	4	0	0	0	0	0
		2	13.254	8.836	17.672	0.000	0.000	0.000	0.000	0.000
6607	133.23	1	10	28	8	6	2	0	0	0
		2	43.030	51.636	12.909	21.515	8.606	0.000	4.303	4.303
6607	137.22	1	60	15	8	11	14	6	3	3
		2	147.816	24.636	24.636	32.848	12.318	4.106	8.212	8.212
6607	137.23	1	5	0	1	0	1	1	0	1
		2	0.000	4.413	0.000	0.000	0.000	0.000	0.000	0.000
6608	130.28	1	8	33	29	27	9	5	1	1
		2	36.940	70.186	33.246	33.246	3.694	7.388	3.694	0.000
6608	130.30	1	83	56	15	8	1	0	2	1
		2	99.441	77.343	7.366	11.049	7.366	0.000	3.683	0.000
6608	133.25	1	11	63	13	3	6	0	1	0
		2	43.308	198.495	14.436	10.827	3.609	0.000	0.000	0.000
6610	120.40	1	2	14	9	4	5	8	6	8
		2	0.000	10.761	7.174	3.587	14.348	17.935	10.761	3.587
6610	130.28	1	2	32	2	0	0	0	0	0
		2	7.128	46.332	0.000	0.000	0.000	0.000	0.000	0.000
6611	120.25	1	1	13	263	294	111	75	40	33
		2	3.621	28.968	318.648	152.082	83.283	83.283	65.178	32.589
6611	137.23	1	1	23	2	1	0	0	0	0
		2	10.935	54.675	0.000	0.000	0.000	0.000	0.000	0.000
6706	110.40	1	0	1	9	0	0	0	0	0
		2	0.000	0.000	3.074	0.000	0.000	0.000	0.000	0.000
6706	120.24	1	5	30	57	13	4	1	0	0
		2	113.004	194.618	116.143	12.556	0.000	0.000	0.000	0.000
6706	120.40	1	4	118	175	65	25	11	5	2
		2	32.175	216.450	187.200	35.100	8.775	5.850	2.925	0.000

$$\tilde{s}_{1j} = \frac{\sum_{k=1}^{m} n_{1jk}}{\sum_{k=1}^{m} n_{2jk}}. \qquad (3)$$

Plots of n_{1jk} and n_{2jk} did not clearly indicate the relation between e_{jk} and n_{2jk}. Thus both methods of estimating s_{1j} were used.

Examination of the data revealed that a linear equation is appropriate to describe the relation between s_{1j} and L_j when $L_j \leqslant 5.75$ mm.

$$\tilde{s}_{1j} = a + bL_j. \qquad (4)$$

Linear regression techniques were used to estimate the parameters, a and b, of the equation.

RESULTS

Table 1 presents catches of anchovy larvae by the type 1 and type 2 nets for each sample. The first two digits of the cruise refer to year and the second two by month. Station notation is explained by Ahlstrom (1966). Larvae greater than 9.75 mm were captured, but the numbers involved were too small to be useful for the study. Estimates by (2) and (3) of s_{1j} are as follows:

L_j(mm)	$\tilde{s}_{1j}(2)$	$\tilde{s}_{1j}(3)$
2.50	0.312	0.367
3.75	0.512	0.603
4.75	0.711	0.699
5.75	0.946	1.057
6.75	0.875	0.916
7.75	0.753	1.021
8.75	1.007	1.226
9.75	0.664	1.087

Plots, Figure 1, of the estimates show that there is a very good linear relation between the estimates and L_j when 2.50 mm $\leqslant L_j \leqslant$ 5.75 mm. When $L_j >$ 5.75 mm $\tilde{s}_{1j}(2)$ decreases while $\tilde{s}_{1j}(3)$ fluctuates about 1. Thus it appears that a linear relation (4) provides an adequate description of the relation between $\tilde{s}_{1j}$ and L_j when 2.50 mm $\leqslant L_j \leqslant$ 5.75 mm. When $L_j >$ 5.75 mm it is assumed that $\tilde{s}_{1j} = 1$. Vannucci (1968) reviewed papers that used the logistic and normal distribution functions which have s_{ij} approaching 1 as an asymptote rather than the discontinuous equation used in this study. The data used in this study are not accurate enough when $L_j >$ 5.75 mm to warrant use of an asymptotic relation. The very good linear relation between L_j and $\tilde{s}_{1j}$ when $L_j \leqslant$ 5.75 mm and the high values of $\tilde{s}_{1j}$ when $L_j =$ 5.75 mm indicate that any deviation from the equation used in this study would cause minor errors when $\tilde{s}_{1j}$ are used to correct catches of anchovy larvae for loss through meshes.

The estimate of a from (2) and (4) is —0.1942, b is 0.1945, and the correlation coefficient, r, is 0.9961. When (3) was used a is —0.1075, b is 0.1850, and r is 0.9814.

Table 2 contains catches of sardine larvae used in the study. Estimates by (2) and (3) of s_{1j} are as follows:

L_j(mm)	$\tilde{s}_{1j}(2)$	$\tilde{s}_{1j}(3)$
2.50	0.375	0.358
3.75	0.385	0.436
4.75	0.817	0.782
5.75	1.754	1.330
6.75	1.275	1.203
7.75	0.881	0.926
8.75	0.584	0.526
9.75	0.873	0.854

The estimates of s_{1j} for sardine larvae are similar to those for anchovy larvae. Thus the same discontinuous function is assumed. The estimate of a from (2) and (4) is —0.2382, b is 0.2107, and r is 0.9320. Estimates obtained when (3) was used are a, —0.2286, b, 0.2084, and r, 0.9639. The resulting curves for both anchovy and sardine larvae are shown in Figure 2. The curves differ little either within or between species. Since the highest value of r, 0.9961, was estimated for anchovy larvae using equation (2), the somewhat arbitrary decision was made to use the results obtained from equation (2).

ESTIMATION OF PORTION OF LARVAE PASSED THROUGH MESHES OF TYPE 1 (0.55-MM MESH) NET

The type 1 net has been the major plankton sampler of the CalCOFI. Estimates of spawning biomass of the northern anchovy population have been based on the ratio of total catches of sardine larvae to total catches of anchovy larvae (Ahlstrom, 1968). If there are major differences in the percentages of sardine and anchovy larvae retained by the net, then the estimates of anchovy spawning biomass may be seriously in error. Ahlstrom (personal communication) believed that his assumption that the two species were sampled equally well was valid because of the similar forms of larvae of the two species and his interpretations of catch curves of larvae of the two species.

Catch (average) curves of anchovy and sardine larvae were calculated from a series of CalCOFI samples taken during the months of January through July during the decade 1951-1960. More than 10,000 samples are involved. Catch curves were calculated for day and night samples separately because of marked differences between the two. The curves were then corrected for nonretention of larvae as follows:

$$n'_{1jko} = n_{1jko}(1/s_{1j}) \qquad (5)$$

where n'_{1jko} = the corrected catch of larvae of size L_j by net type 1 in the kth time of day, and oth species.

$$k = \begin{cases} 1 \text{ for night samples} \\ 2 \text{ for day samples} \end{cases}$$

$$o = \begin{cases} 1 \text{ for anchovy} \\ 2 \text{ for sardine} \end{cases}$$

The corrected and uncorrected curves plotted on a semilogarithmic scale are shown with n_{1jko} and n'_{1jko} expressed in percent of total in Figures 3-6. The corrected curve for anchovy larvae caught at night shows a slight increase in the rate of decline with size. The corrected curve for anchovy caught during the day is essentially linear as is the corrected catch curve for sardine larvae caught during the night. The corrected catch curve for sardine larvae caught during the day shows a decreasing rate of decline with size. In all cases the corrected curves show little indication of undersampling of small larvae.

The following equation was used to estimate the portion of larvae not collected by the type 1 net because of passage through the mesh:

$$P_{1o} = \frac{\sum_{jk} \sum n_{1jko}}{\sum_{jk} \sum n'_{1jko}} \qquad (6)$$

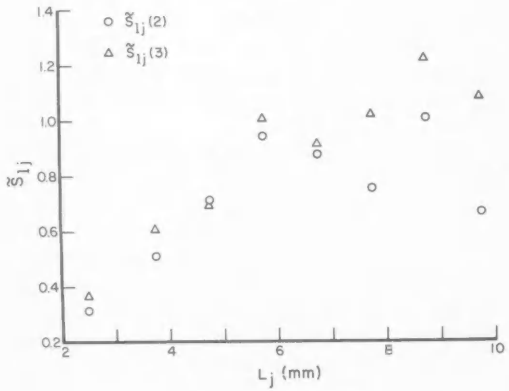

FIGURE 1.—Scatter diagram of estimates of mesh retention by type 1 (0.55-mm mesh) net using equation (2) ($S_{1j}(2)$), mesh retention using equation (3) ($s_{1j}(3)$), and standard length (L_j) for northern anchovy larvae.

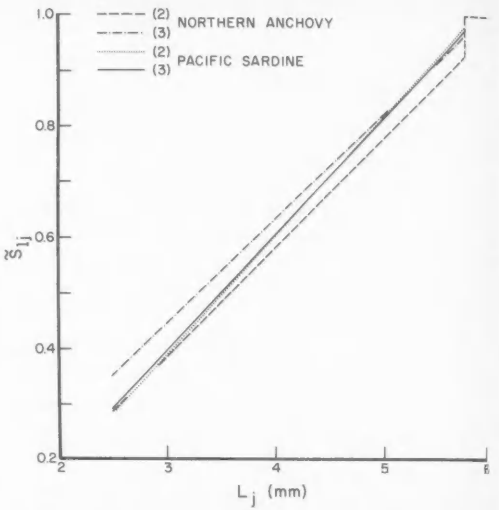

FIGURE 2.—Estimates of mesh retention by type 1 (0.55-mm mesh) net (s_{1j}) against standard length (L_j) for larvae of northern anchovy and Pacific sardine using equations (2) and (3).

where $1-P_{io}$ = portion of larvae of species o not sampled by type i net because of passage through meshes.

Equation (6) implies that an equal number of night and day samples are taken. This is approximately correct. The estimate of P_{1o} for anchovy is 0.60. The estimate of P_{1o} for sardine is 0.67. Thus anchovy larvae are undersampled by about 12% relative to sardine larvae because of differences in mesh retention and size composition.

CATCH CURVE OF TYPE 3 (0.505-MM MESH) NET

Figure 7 shows the catch curve plotted on a semilogarithmic scale of anchovy larvae caught by the type 3 net during 1969 by the CalCOFI. This data is preliminary (P. E. Smith, personal communication) and catches have not been separated by day and night. The interesting feature of this curve is that it is essentially linear

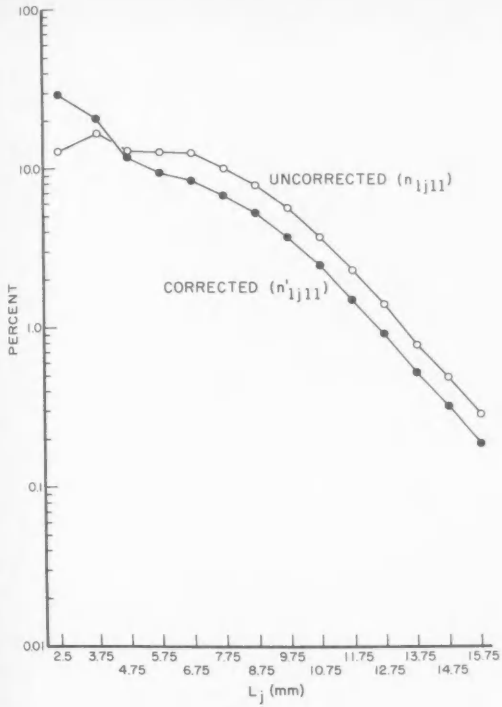

FIGURE 3.—Corrected (n'_{1j11}) and uncorrected (n_{1j11}) catches by standard length (L_j) of northern anchovy taken at night with type 1 (0.55-mm mesh) net. Catches are expressed in percent of total.

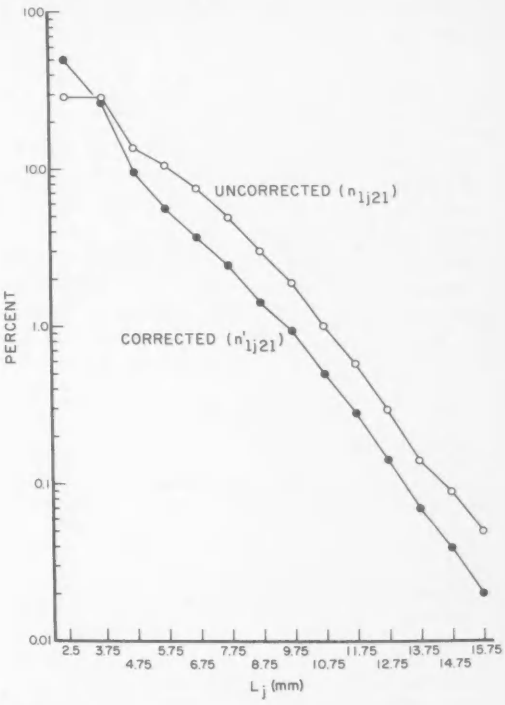

FIGURE 4.—Corrected (n'_{1j21}) and uncorrected (n_{1j21}) catches by standard length (L_j) of northern anchovy taken during day with type 1 (0.55-mm mesh) net. Catches are expressed in percent of total.

with size. This indicates that few if any small anchovy larvae escape capture by passing through the meshes. Thus a 10% decrease in mesh size and a large decrease in the variance of mesh size changed P_{i1} from 0.60 to about 1. The difference in P_{i1} between the type 1 and type 3 nets means that total catches of anchovy larvae by the type 1 net should be multiplied by 1.7 to be comparable to catches of anchovy larvae by the type 3 net.

DISCUSSION

The similarity of the catch curves of anchovy larvae caught by the type 3 net and the corrected catch curve for the type 1 net suggests that the estimates of s_{1j} are reasonably accurate. It would be a remarkable coincidence otherwise as the data are independent.

It is interesting that the type 3 (0.505-mm mesh width) net apparently retains most if not all anchovy larvae, for the body depth at the insertion of the pectoral fin of 3.75-mm anchovy larvae is about 0.35 mm (P. E. Smith, personal communication) which is considerably less than the mesh width. Smith, Counts, and Clutter (1968) summarized the results of Saville (1958) by concluding that an organism must be wider than the mesh diagonal to be completely retained. A conclusion of this study is that the "diagonal rule" is too conservative for slowly towed nylon nets. Heron (1968) concluded that mesh variability is a very important factor in-

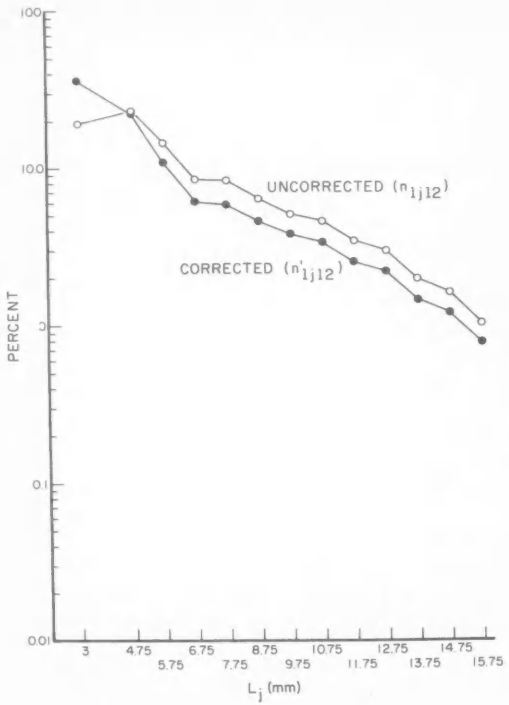

FIGURE 5.—Corrected (n'_{1j12}) and uncorrected (n_{1j12}) catches by standard length (L_j) of Pacific sardine taken at night with type 1 (0.55-mm mesh) net. Catches are expressed in percent of total.

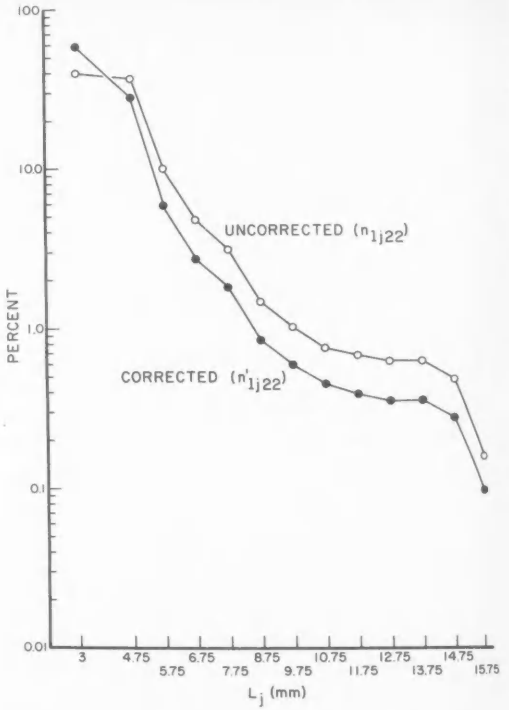

FIGURE 6.—Corrected (n'_{1j22}) and uncorrected (n_{1j22}) catches by standard length (L_j) of northern anchovy taken during day with type 1 (0.55-mm mesh) net. Catches are expressed in percent of total.

fluencing escapement and implied that the coefficient of variation of mesh width is greater for silk than nylon nets. The results of this study agree with Heron's conclusions.

The results indicate that two similar types of sampling gear have greatly different mesh retention properties for anchovy larvae. This implies that considerable care should be taken in the selection of sampling gear if quantitative estimates of the abundance of fish larvae are desired. The similarity in mesh retention shown for anchovy and sardine larvae may be due to the fact that the larval forms are very similar. However the diversity of forms found in fish larvae is tremendous. Mesh retention should be estimated before quantitative estimates of the relative abundance of larvae of different species of fish are attempted. The results indicate that adequate estimates of mesh retention can be made from less than 30 samples containing the desired species of fish larvae. If the mesh retention curve is curvilinear in the region of fish larvae of minimum size, more samples may be necessary.

The reasoning of Hjort (1926) in expecting a critical period in the early life of fish larvae is intuitively pleasing. Hunter (1972) showed experimentally that a much higher density of food organisms is necessary for survival of 4- to 6-mm anchovy than for larger larvae. However, there is no indication of a critical period at the 4- to 6-mm sizes in this study, i.e., there are no major

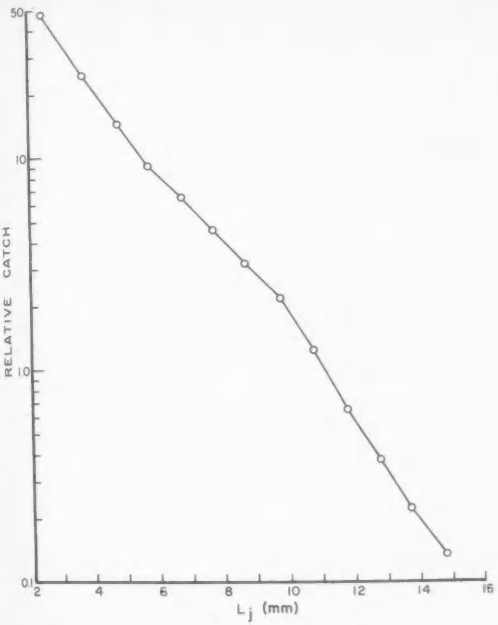

FIGURE 7.—Catches of northern anchovy by standard length (L_j) taken by type 3 (0.505-mm mesh) net.

changes in the slopes of the catch curves. However, since the catches are plotted with size rather than age, a faster rate of growth at small sizes relative to large sizes could cause small size larvae to be relatively undersampled. If this were the case, a critical period could occur but not be indicated by catches plotted with size. Kramer and Zweifel (1970) indicated that the growth rate of anchovy larvae increases rather than decreases with size during the first few millimeters of growth. Another factor that could influence the catch rate of larvae differently with size is avoidance of the net. However, experience indicates that avoidance increases with size (Lenarz, in press). Thus, the large larvae should be relatively undersampled. I conclude, therefore, that available data does not provide any evidence of the critical period for sardine or anchovy larvae. This conclusion is in agreement with other authors that have examined catch curves of fish larvae, e.g., Marr (1956).

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THE INCREASE IN SPAWNING BIOMASS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

PAUL E. SMITH[1]

ABSTRACT

The northern anchovy, *Engraulis mordax*, is a common fish off the west coast of North America. Its biomass has increased markedly since 1951. The various methods of deriving anchovy spawner biomass from the sardine spawner biomass and analogous census estimates of sardine and anchovy larvae are reviewed. A new compilation of anchovy and sardine larval data is presented for 1940, 1941, 1949, 1950, and 1951-69. The effect of several errors of estimate are examined and it is concluded that none is important enough to affect measurably the trend of increase between 1951 and 1966. Lastly, a current interpretation of the larval survey data is used to estimate the spawning biomass of both sardine and anchovy.

The northern anchovy (*Engraulis mordax* Girard) is a common pelagic schooling fish off the west coast of North America between British Columbia and Baja California (lat 53°N to 22°N). The fishery for northern anchovy has usually been small relative to the Pacific sardine (*Sardinops caerulea* (Girard)) off California but the anchovy catch has been increasing since the late 1930's (Figure 1). Following the collapse of the sardine fishery in the early 1950's, the catch of anchovy exceeded that of sardine. The further decline of sardine catch and the eventual moratorium on sardine, combined with a limited reduction fishery on anchovy, have again allowed the anchovy fishery to exceed that of sardine since the mid-1960's (Messersmith and Associates, 1969).

Routine planktonic larva sampling since 1951 shows an increase in the number of anchovy larvae (Murphy, 1966; Ahlstrom, 1966, 1968) and the present consensus estimate of the spawning population of northern anchovy is about 5 million tons for 1966, the last year for which complete data are available. The same sample data for the Pacific sardine now indicate an extremely small number of larvae and the spawning biomass of the northern subpopulation of the sardine may now be less than 5,000 tons. All anchovy biomass estimates must now be referred to analogous sardine biomass estimates based on the sardine fishery and on sardine and anchovy egg and larva surveys because no fishery-based estimate of anchovy biomass has yet been made: this becomes increasingly difficult and imprecise as the sardine "reference" population diminishes.

The purposes of this paper are to:

1) review the estimates of spawner biomass of the anchovy;
2) present a summary of the incidence of larval anchovy by region and season since 1951;
3) examine the effects of three spawning behavior models on the estimates of spawning biomass;
4) establish a standard reference period for the determination of anchovy biomass without further consideration of the current size of the sardine population.

PREVIOUS ESTIMATES OF ANCHOVY BIOMASS

Messersmith and Associates (1969, p. 9) tabulated all the estimates of anchovy spawning biomass for the years 1940-66. Ahlstrom (MRC,

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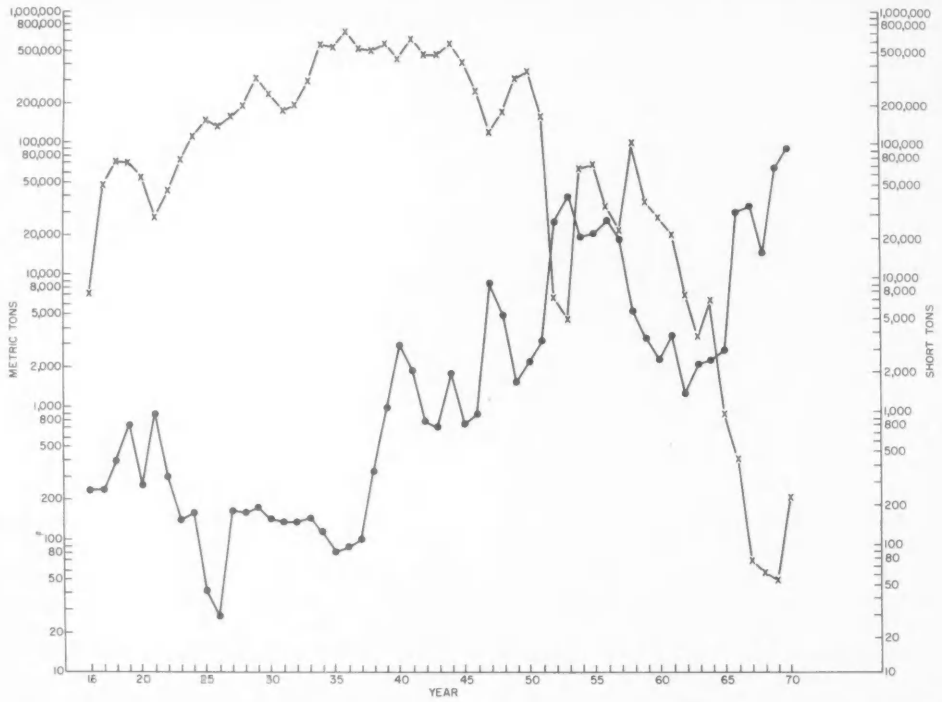

FIGURE 1.—The annual catch of sardine (crosses) and anchovy (solid circles) in the California Current system since 1916. Whole fish reduction was essentially banned in 1919 and a limited whole fish reduction fishery was opened in 1965.

1964)[2] in an informal statement, emphasized the changing ratio of anchovy larvae to sardine larvae from 3.1 to 1 in 1951 to 46.8 to 1 in 1959. In a similarly informal statement, MacGregor (MRC, 1964) described a method for estimating the spawning biomass of pelagic spawning species. That portion of his statement which is related to sardine and anchovy follows:

> Egg and larval surveys conducted over the years have given us a basis for estimating the total numbers of eggs and larvae produced each year in the CalCOFI (California Cooperative Oceanic Fisheries Investigations) survey area for a number of fish species. We also have information on the fecundity of a number of these species and from the combined data can estimate the biomass of spawning adult fish on each species. The number of eggs a fish will produce at one spawning appears to be directly related to the weight of the fish. Thus, we can compute the numbers of eggs produced in one spawning by a ton of female fish as follows:

Species	Millions of eggs
Anchovy	525
Sardine	241

> The above figures represent female fish only. If we assume, as evidence indicates, that for each ton of adult females there is also present a ton of adult males, we would have to divide the number of eggs produced

[2] A review of estimates and procedures was conducted for the California Marine Research Committee (MRC) in 1964 and the texts of the presentations are to be found there. Statements and calculations were neither edited nor formally derived. Quotations from the Appendix to these minutes will be regarded as informal and cited (MRC, date).

by 2 to obtain the number of eggs produced [in one spawning][3] by one ton of adult fish. If we further assume that . . . . about half the [adult] sardine population spawns twice [a year] (average 1½ times) and the anchovy [adult] population spawns 2 or 3 times a year (average 2½ times), we would also multiply millions of eggs by 1½ for the sardine and 2½ for the anchovy. On the above basis the total number of eggs produced by one ton of adult fish of both sexes in one year would be as follows for each species:

Species	Millions of eggs
Anchovy	656
. . . .	. .
Sardine	181
. . . .	. .

It may be seen from the above that, although numbers of eggs or larvae in the plankton may be used as an index of adult abundance, a sardine egg in the plankton represents 3½ times . . . as much adult biomass as an anchovy egg. Estimates of the average biomass of each . . . species for the 3-year period 1955-57 and the average commercial landings for the same period are as follows:

Species	Biomass (tons)	Catch (tons)
Anchovy*	750,000	29,686
. . . . .	. . . . .	. . . .
Sardine	254,000	51,508

* Anchovy larvae caught were used as an estimate of eggs. This may have resulted in underestimation by a factor of 2. Application of this factor brings this biomass of anchovies into line with the material in Murphy's (MRC, 1964) estimate of the anchovy harvest . . . .

[3] In brackets added for clarification.

In another informal statement Radovich (MRC, 1965) cited the change in anchovy to sardine larval ratios (Ahlstrom, MRC, 1964) and stated ". . . in this 8-year period the anchovy maintained its population level fifteen times better than the sardine . . . ." He further pointed out that the necessary ratio of annual survival rates to attain this was 1.4. Should this difference in survival be in the larval stage, the MacGregor (MRC, 1964) biomass estimate should be divided by 1.4 or roughly 1.5, resulting in an estimate of about 1 million tons.

Murphy (MRC, 1964) used an anchovy spawner biomass estimate which was essentially double MacGregor's (MRC, 1964) because he believed that the escapement of anchovy larvae through the mesh of the standard CalCOFI silk net exceeded the escapement of the sardine larvae enough to cancel the effect of anchovy fecundity exceeding sardine fecundity. Thus Murphy's calculation (1966, p. 60) of anchovy spawner biomass for the period 1955-57 was 3.3 million short tons as compared to MacGregor's 1.5 million short tons and Radovich's 1.0 million short tons for the same 3-year period. An estimate by Murphy's method for 1958 would be 5.1 million short tons.

Ahlstrom (1968) estimated that the 1958 anchovy biomass was between 1.80 and 2.25 million short tons and observed further that the biomass had reached a plateau of 4.5 to 5.625 million short tons in the mid-1960's.

TABLE 1.—Comparison of data used for estimating the spawning biomass of northern anchovy.

	Standard haul summation[1]		Summation of average quarterly estimates[2]		Larval census estimates[3]		Standard haul summations[4]	
	Anchovy	Sardine	Anchovy	Sardine	Anchovy	Sardine	Anchovy	Sardine
1951	29,551	11,068	9,826	3,689	15,101	5,774	29,552	11,066
1952	59,626	19,179	20,581	6,437	17,071	5,466	63,057	24,559
1953	99,160	14,400	34,314	4,924	23,680	4,020	103,928	15,055
1954	161,241	26,914	56,665	9,364	38,415	7,297	161,254	26,914
1955	140,183	14,121	51,096	5,554	37,658	4,341	140,183	14,121
1956	134,931	15,523	51,438	5,179	38,508	3,895	134,931	15,523
1957	146,631	9,833	53,921	3,415	40,441	2,432	146,631	9,833
1958	205,733	11,427	75,120	3,845	56,928	2,831	205,457	11,423
1959	206,753	5,374	72,732	2,072	54,168	1,159	206,000	5,308
1960	289,860	8,012	97,602	3,099				
1961	97,103*	1,708*	97,103	1,708				
1962	212,675*	2,258*	212,675	2,258				
1963	205,838*	1,349*	205,838	1,349				
1964	166,517*	2,757*	166,517	2,757				
1965	258,781*	3,573*	258,781	3,603				
1966	380,420	5,640	161,333	2,211				

[1] Ahlstrom 1966, tables 2 and 4 (1965, 1966, numbers from current unpublished data).
[2] Ahlstrom, 1966, 1968.
[3] Ahlstrom, 1968.
[4] Murphy, 1966.
* Quarterly cruises rather than monthly.

TABLE 2.—Stations and pooled areas within each region as used in this study.

Regional name	Pooled areas	Stations
Central California Inshore	6.5	60.52
18 stations	5,270 miles²	60.55
4 pooled areas		63.52
19,970 miles²		63.55
		67.50
		67.55
	6.6	60.60
	4,800 miles²	63.60
		67.60
	7.5	70.52 (51)
	5,100 miles²	70.55 (53)
		73.51 (50)
		73.55 (53)
		77.50 (51)
		77.55
	7.6	70.60
	4,800 miles²	73.60
		77.60
Central California offshore	6.7	60.70
6 stations	6.8	60.80
6 pooled areas	6.9	60.90
28,800 miles²	7.7	70.70
	7.8	70.80
	7.9	70.90
Southern California inshore	8.4	82.47
19 stations	4,589 miles²	83.40
3 pooled areas		83.43
15,348 miles²		87.35
		87.40
		87.45
	9.3	90.28
	5,989 miles²	90.30 (32)
		90.37
		93.27 (28)
		93.30
		97.30
		97.32
		97.35
	9.4	90.45
	4,770 miles²	93.40
		93.45
		97.40
		97.45
Southern California offshore	8.5	80.51 (52)
16 stations	4,747 miles²	80.55
4 pooled areas		83.51
19,147 miles²		83.55
		87.50
		87.55
	8.6	80.60
	4,800 miles²	83.60
		87.60
	9.5	90.50
	4,800 miles²	90.55 (53)
		93.50
		93.55
		97.50
		97.55
	9.6	90.60
	4,800 miles²	93.60
		97.60
Southern California seaward	8.7	80.70
18 stations		83.70
6 pooled areas		87.70
28,800 miles²	8.8	80.80
		83.80
		87.80
	8.9	80.90
		83.90
		87.90
	9.7	90.70
		93.70
		97.70
	9.8	90.80
		93.80
		97.80
	9.9	90.90
		93.90
		97.90
Baja California inshore	10.3	100.29
29 stations	5,535 miles²	100.30
4 pooled areas		100.35
21,089 miles²		103.30
		103.35
		107.32
		107.35
	10.4	100.40
	4,800 miles²	103.40
		103.45
		107.40
	11.3	110.33 (32)
	5,956 miles²	110.35
		113.30
		113.35
		117.26
		117.30
		117.35
		118.39
		119.33
		120.25
		120.30
		120.35
	11.4	110.40
	4,798 miles²	110.45
		113.40
		113.45
		117.40
		117.45
Baja California offshore	10.5	100.50
15 stations	4,800 miles²	103.50
4 pooled areas		107.50
19,200 miles²	10.6	100.60
	4,800 miles²	103.60
		107.60
	11.5	110.50
	4,800 miles²	110.55
		113.50
		113.55
		117.50
		117.55
	11.6	110.60
	4,800 miles²	113.60
		117.60
Baja California seaward	10.7	100.70
19 stations	4,800 miles²	103.70
6 pooled areas		107.70
28,800 miles²	10.8	100.80
	4,800 miles²	103.80
		107.80
	10.9	100.90
	4,800 miles²	103.90
		107.90
	11.7	110.70

TABLE 2.—Continued.

Regional name	Pooled areas	Stations
	4,800 miles²	113.70
		117.70
		117.75
	11.8	110.80
	4,800 miles²	113.80
		117.80
	11.9	110.90
	4,800 miles²	113.90
		117.90
South Baja inshore	12.3	123.37
22 stations	4,459 miles²	127.34
5 pooled areas	12.4	120.40
22,790 miles²	4,800 miles²	120.45
		123.42
		123.45
		127.40
		127.45
	13.2	133.25
	3,931 miles²	137.23
	13.3	130.30
	4,800 miles²	130.35
		133.30
		133.35
		137.30
		137.35
	13.4	130.40
	4,800 miles²	130.45
		133.40
		133.45
		137.40
		137.45
South Baja offshore	12.5	120.50
16 stations	4,800 miles²	120.55
4 pooled areas		123.50
19,200 miles²		123.55
		127.50
		127.55
	12.6	120.60
	4,800 miles²	123.60
		127.60
	13.5	130.50
	4,800 miles²	130.55
		133.50
		137.50
	13.6	130.60
	4,800 miles²	133.60
		137.60
South Baja seaward	12.7	120.70
3 stations	12.8	120.80
3 pooled areas	12.9	120.90
14,400 miles²		

Murphy (1966) estimated the biomass of the spawning stocks of sardine from 1932 to 1959. He also compared the anchovy:sardine larval ratio from 1951 to 1959 and graphically compared this with the larval ratio over a portion (about 20%) of their joint range in 1940 and 1941 (p. 65). The striking decline of the sardine, and the increase of the anchovy biomass, has stimulated speculation on the biological interactions of these species and the MRC (Marine Research Committee of California) has a standing recommendation that 200,000 tons of anchovies and 10,000 tons of sardines be harvested in an experimental attempt to foster the recovery of sardines. It is the primary goal of this recommendation to restore and maintain the balance of sardines and anchovies in the California Current system by manipulation of fishing effort.

The estimates of spawning biomass of the northern anchovy have been based on the spawning biomass of the Pacific sardine as derived from the fishery (Murphy, 1966; Ahlstrom, 1968) and on the assumed relationship between sardine and anchovy fecundity, survival, and escapement of larvae through the meshes of the CalCOFI standard silk survey net (Lenarz, 1972). For convenience, the larva data for all estimates to date are listed in Table 1. A series of stations off southern California was occupied in 1940 and 1941, and the anchovy:sardine ratios were 1.18 (13,962 anchovy to 11,862 sardines) and 1.66 (12,560 anchovy to 7,564 sardines) respectively. The 1940, 1941, 1949, and 1950 data will be referred to later in a section on interaction of sardine and anchovy.

METHOD OF DATA ASSEMBLY

The method of assembling the estimates of larval abundance for this paper differs from that of Sette and Ahlstrom (1948) and Ahlstrom (1954, 1966, 1967, 1968). Two methods of assembly were used previously: the "census estimate" and the "standard haul summation." In the "census estimate" each larva sample count was weighted by the area of a polygon formed by construction of "perpendicular bisectors of lines drawn from the station to each of all surrounding stations" (Sette and Ahlstrom, 1948, p. 521; Ahlstrom, 1968).

$$C_k = 10\sum_{j=1}^{n}\left[\sum_{i=1}^{m} A_s\left(a_i^{-2}\, b_i^{-1}\, c_i\, d_i\right)\right]_j \qquad (1)$$

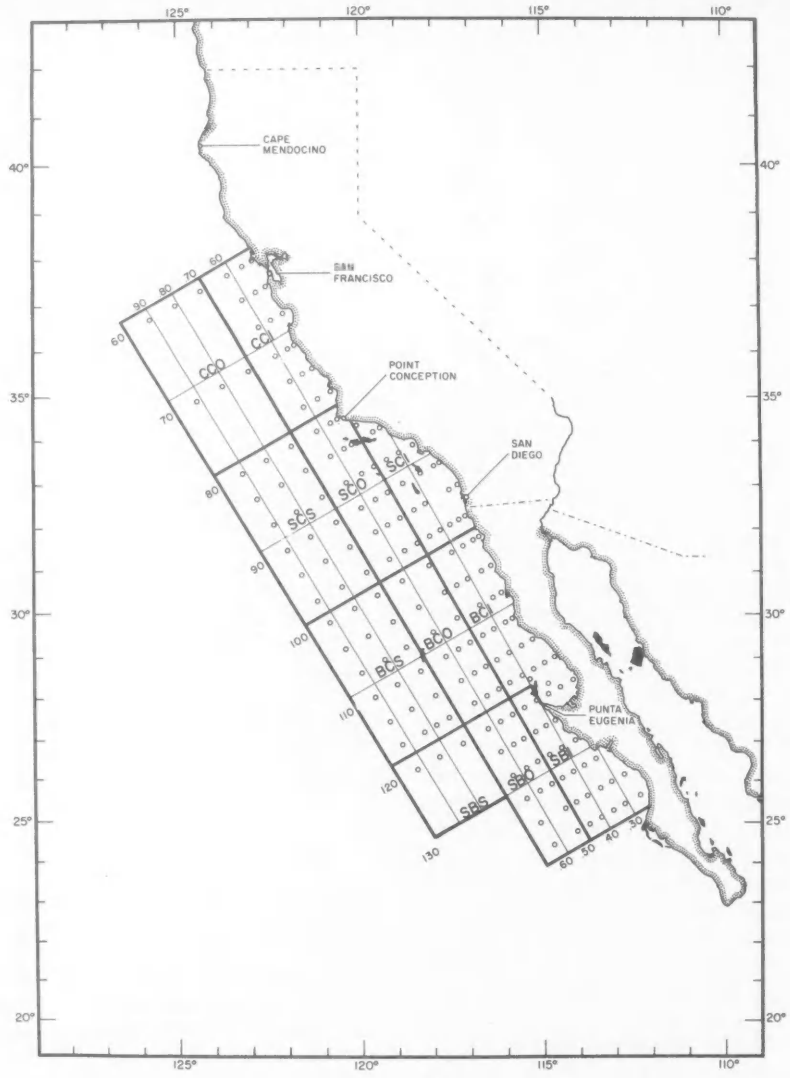

FIGURE 2.—The selected stations of the CalCOFI grid (see Tables 2 and 3) and the regional boundaries defined for this paper. Columns of stations are indicated .30, .40 . . . .90, and rows of lines are indicated 60, 70, . . . 130. The first two letters of each three-letter group stand for coastal bands, i.e., central California (CC), Southern California (SC), Baja California (BC), South Baja (SB) while the last letter of the three stands for offshore zones roughly parallel to the coast, inshore (0-80 miles from the coast, "I", offshore (80-160 miles from the coast, "O"), and seaward (160-280 miles from the coast, "S"), so that the three letters SCI stand for the southern California inshore region.

TABLE 3.—Description of CalCOFI regions used in this analysis.

Regional name	Stations	Pooled areas	Square miles	Area factor
Central California inshore	18	4	19,970	6.85×10^9
Central California offshore	6	6	28,800	9.88
Southern California inshore	19	3	15,348	5.26
Southern California offshore	18	4	19,147	6.57
Southern California seaward	18	6	28,800	9.88
Baja California inshore	29	4	21,089	7.23
Baja California offshore	15	4	19,200	6.58
Baja California seaward	19	6	28,800	9.88
South Baja inshore	22	5	22,790	7.82
South Baja offshore	16	4	19,200	6.58
South Baja seaward	3	3	14,400	4.94
Totals	183	49	237,544	81.48

TABLE 4.—Equivalent station list off southern California for 1940, 1941, and 1950-72.

Southern California inshore			Southern California offshore		
Station no. used in 1940	Station no. used in 1941	Nearest present station no.	Station no. used in 1940	Station no. used in 1941	Nearest present station no.
02	12	82.47	04	15	80.51
01	11	83.40	05	16	80.55
08	23	83.43	03	13	83.51
10	21	87.35	13	14	83.55
17	22	87.40	24	24	87.50
11	34	87.45	12	25	87.55
21	30	90.28	06	28	80.60
19	31	90.30	09	27	83.60
20	32	90.37	18	26	87.60
22	41	93.27	23	35	90.50
28	51	90.30	31	36	90.55
--	60	97.30	39	45	93.50
35	61	97.32	40	46	93.55
36	62	97.35	41	64	97.50
30	33	90.45	14	55	97.55
29	52	93.40	32	37	90.60
34	54	93.45	25	47	93.60
37	63	97.40	33	--	97.60
38	53	97.45			

where A_s = area of a polygon constructed of perpendicular bisectors of lines between station "i" and all adjacent stations expressed as number of 10 m^2 areas

C_{kf} = estimate of abundance of larvae in year "k" and "f" takes the value of the number of the equation

C_i = number of larvae in "ith" sample

a_i = area of mouth of the net used at the "ith" station

b_i = length of tow in meters estimated from a calibrated flow meter at station "i"

d_i = tow depth in meters estimated from the wire angle at maximum wire out at station "i"

m = number of stations

n = number of monthly cruises.

In the "standard haul summation" approach the sums of all tows on regularly occupied stations for each monthly cruise were totaled for the year without weighting for represented area.

$$C_k = 10 \sum_{j=1}^{n} \left[\sum_{i=1}^{m} \left(a_i^{-2}\ b_i^{-1}\ c_i\ d_i \right) \right]_j . \quad (2)$$

To accommodate the quarterly cruises Ahlstrom (1966, 1968) established a modification of this in which the quarterly averages of 1 to 3 monthly cruise summations were added to make an

annual total (Ahlstrom, 1966, Table 8; 1968, Table 3).

$$C_k = 10 \sum_{q=1}^{4} \left\{ \sum_{j=1}^{n} \left[\sum_{i=1}^{m} \times \left(a_i^{-2}\, b_i^{-1}\, c_i\, d_i \right) \right]_j n^{-1} \right\}_q . \quad (3)$$

Murphy (1966) used the monthly version of Ahlstrom's standard haul summation (Table 1).

The method used here is called the "regional census estimate"

$$C_{k4} = 10\, A_r m^{-1} \left[\sum_{i=1}^{m} \left(a_i^{-2}\, b_i^{-1}\, c_i\, d_i \right) \right] \quad (4)$$

where C_{k4} = estimate of abundance of larvae in region "r" in each quarter

A_r = Area of region "r" in numbers of 10 m² areas.

This method of assembly combines the simplicity of the "standard haul summation" and the areal weighting of the previously used census estimates. The regional census estimate consists of the mean number of larvae per standard area (10 m² sea surface) of all stations taken within a region for a quarter of the year times the number of standard areas within the region. The same 183 stations or nearby alternates were used within the routinely occupied area as defined by Smith, Ahlstrom, and Casey (1970, Figure 1). The selected stations and acceptable alternates are listed in Table 2 and the regions are illustrated in Figure 2 and defined by area and area factor in Table 3.

The 1940 and 1941 stations have been assigned to the two southern California regions (Table 4) in which these cruises were conducted. The number of stations per unit area has been held nearly constant by the elimination of excess stations in the early cruises. The 1949 station equivalents are listed in Table 5. From 1950 to 1972 stations have been standard in placement.

TABLE 5.—Equivalent station list for the CalCOFI survey pattern for 1949 and 1950-72.

Area	Station no. used in 1949	Nearest present station no.
Central California inshore	601	63.58
	701	72.56
Central California offshore	602	62.68
	603	61.78
	604	61.87
	702	71.66
	703	71.76
	704	71.85
Southern California inshore	901	92.39
Southern California offshore	801	82.57
	902	92.48
	903	92.58
Southern California seaward	802	82.67
	803	82.77
	804	82.87
	904	92.68
	905	92.78
Baja California inshore	1001	101.34
	1002	101.44
	1101	111.38
	1102	111.48
Baja California offshore	1003	102.54
	1004	102.64
	1103	111.58
Baja California seaward	1005	102.74
	1006	102.84
	1007	102.94
	1104	111.68
	1105	112.78
	1106	112.88
	1107	112.98
Southern Baja inshore	1201	122.44
Southern Baja Offshore	1202	122.53
Southern Baja seaward	1203	123.63
	1204	123.73
	1205	124.83

Extra cruises, additional lines, and stations on lines have been added periodically, resulting in some increase in station density in some areas. To stabilize sampling effort and remove possible effects of added effort nearshore, all but 183 stations and their nearby equivalents have been eliminated from further consideration for the 16-year compilation of regional census estimates. The number of stations eliminated each year are summarized in Table 6.

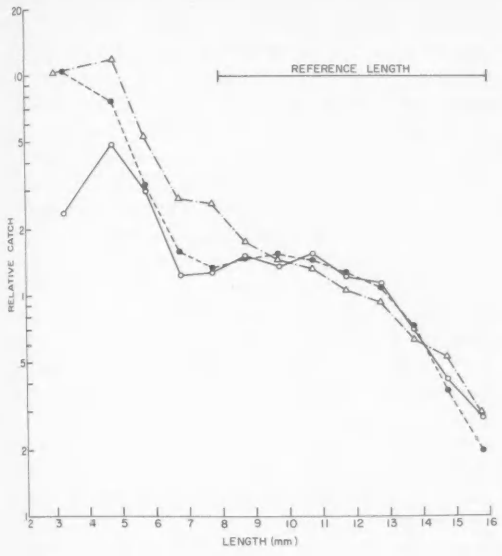

FIGURE 3.—The size frequency of sardine larvae caught in the CalCOFI standard silk net (0.55 mm). The triangle dot-dash curve represents the 1951-60 catch from the selected stations in all eleven regions; the black dot-dash curve represents the 1940 catch from selected stations in the southern California inshore and offshore region and the clear dot solid line represents the 1941 catch from the same two regions. Relative catch refers to the catch at a standard size group (3.00, 3.25 (1940-41), 4.75, 5.75 ... 15.75 mm), divided by the average catch from size groups 8.75 to 15.75.

ESCAPEMENT AND AVOIDANCE BY ANCHOVY AND SARDINE LARVAE

The chief errors causing underestimates of C for both anchovy and sardine larvae are those attributable to larvae "escaping" through the meshes of the standard plankton net (see Lenarz, 1972, p. 839) and larvae "avoiding" the mouth of the net (Silliman, 1943; Ahlstrom, 1954, 1959; Clutter and Anraku, 1968). While "escapement" and "avoidance" are important biases to consider in the study of larva growth and mortality, I consider them beyond the scope of this paper. The estimate of anchovy biomass is based on a relative estimate of the number of anchovy larvae and sardine larvae. I must treat escapement and avoidance briefly, since they act differently on the anchovy and sardine and vary from season to season and with changes in sampling gear.

Lenarz (1972) found no appreciable difference in size-specific escapement of sardine and anchovy through net apertures. However, newly hatched anchovy larvae are considerably smaller than sardine larvae. This leads to a variation in the degree of bias (Murphy, 1966) to such escapement. In Figure 3 the catch of all standard sizes of sardine is related to the average catch between 8.75 and 15.75 mm, a size range I assume to be completely retained on 0.55-mm mesh width silk. The primary line is the average size composition for the period 1951-60 for the sardine. The size composition of the 1940

TABLE 6.—Stations eliminated from data assembly for regional census estimates.

Year	No. of stations occupied	183 stations reported each cruise	Stations not reported	Percent reported
1951	1,436	1,026	410	71.4
1952	1,376	1,167	209	84.8
1953	1,346	1,137	209	84.5
1954	1,473	1,217	256	82.6
1955	1,425	1,121	304	78.7
1956	1,399	1,129	270	80.7
1957	1,493	1,165	328	78.0
1958	1,851	1,276	575	68.9
1959	2,182	1,574	608	72.1
1960	1,810	1,305	505	72.1
1961	953	699	254	73.3
1962	920	659	261	71.6
1963	881	659	222	74.8
1964	877	680	197	77.5
1965	1,099	658	441	59.9
1966	1,979	1,487	492	75.1

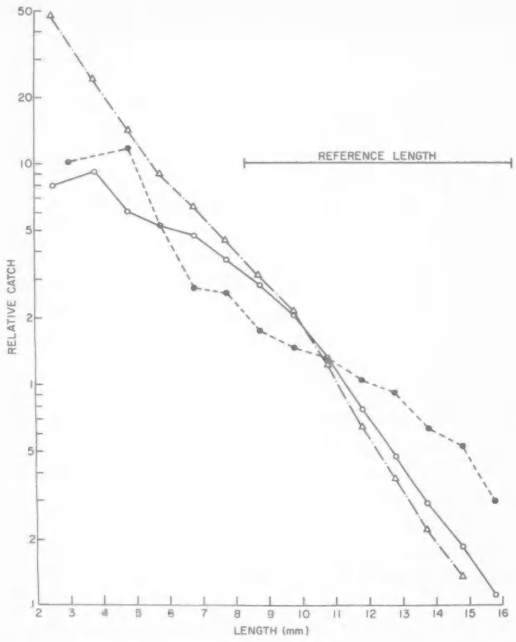

FIGURE 4.—The size frequency of sardine and anchovy larvae. The black dot-dash line is sardine larvae caught in the standard CalCOFI silk net between 1951 and 1960 in all regions from January to June inclusive. The clear dot solid line is anchovy larvae caught in the standard CalCOFI silk net between 1951 and 1960, in all regions from January to June inclusive. The triangle dot-dash line is anchovy larvae caught in the new CalCOFI nylon net (0.505-mm nylon rather than 0.55-mm silk) from January to June 1969 in all regions.

and 1941 sardine catches are included for later reference. In Figure 4, the 1951-60 size composition of sardine is compared to the anchovy for the same period. Anchovy retention in a new net with smaller, more regular meshes (0.505-mm nylon) and more mesh area is included for comparison. All samples reported in the size frequency graphs are from the first half of the year to facilitate comparison with earlier samples and eliminate the effects of poor sampling coverage in the latter half of the year.

Ahlstrom (1954) acknowledged that larger larvae may avoid capture at night as in the daytime. Avoidance is more pronounced in the daylight. In the sardine the night-to-day ratio of catches increases 0.6971 per mm of growth after 4.75 mm (Ahlstrom, 1954, p. 129). Similarly, the anchovy night-to-day catch ratio increases 0.64 for each millimeter growth after 3.5 mm (Ahlstrom, 1959, p. 136). Lenarz (in press) described the annual and diurnal variation in size specific catch rate for sardine, anchovy, hake, and jack mackerel. An important source of variability in avoidance bias is a shift of spawning season. For example, length of day varies from 9.6 hr in winter to 14.8 hr in summer at the latitude of San Francisco near the northern boundary of the survey grid and from 10.6 to 13.7 hr off south Baja California at the southern boundary of the sample grid (54% and 29% respectively). For the 10-year period, 1951-60, the ratio of night-caught to day-caught larvae was 1.72 for sardines and 2.45:1 for anchovy. When the average catch per positive tow by month is corrected for day length at San Francisco the anchovy:sardine ratio changes from 2.96:1 to 3.75:1 for the same decade. A proportionate shift of anchovy spawning toward June would for example, accentuate this difference.

The importance of avoidance and escapement

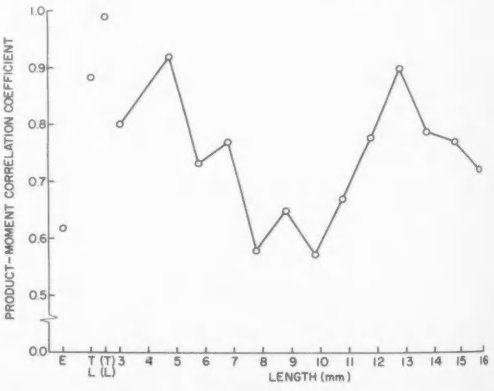

FIGURE 5.—The correlation coefficient between the annual total regional census estimates of sardine eggs and larvae by size class with the Murphy (1966) sardine biomass estimates. The first point is for total eggs, 1951-59; the second point is for total larvae, 1951-59; the third point is for total larvae with 1953 and 1959 censored. The succeeding points are for standard-size classes for all years 1951-59.

TABLE 7.—A comparison of the regional census estimate (A), separately weighted nearshore (B), and 1 month per quarter sampling (C), in the southern California inshore region, 1951-60.

		Winter	Spring	Summer	Fall	Total	Annual rank
1951	A	135	609	111	540	1,395	9
	B	175	879	92	441	1,587	9
	C	289	251	76	276	892	10
1952	A	87	261	314	134	796	10
	B	70	229	336	119	754	10
	C	52	315	531	122	1,020	9
1953	A	578	184	763	1,904	3,429	5
	B	519	139	734	1,409	2,801	6
	C	163	339	1,089	728	2,319	8
1954	A	3,123	516	519	237	4,395	3
	B	1,006	445	412	180	2,043	7
	C	2,577	332	934	149	3,992	5
1955	A	2,012	1,074	849	150	4,085	4
	B	1,682	1,006	737	117	3,542	4
	C	1,941	930	1,111	55	4,037	4
1956	A	236	1,166	708	156	2,266	8
	B	186	1,009	635	117	1,947	8
	C	302	1,632	708	129	2,771	7
1957	A	3,314	3,601	791	267	7,973	1
	B	3,650	3,264	933	238	8,085	1
	C	4,951*	4,060	791	154	9,956	1
1958	A	2,316	2,912	403	63	5,694	2
	B	2,186	3,226	417	36	5,865	2
	C	1,753	4,246	554	51	6,604	2
1959	A	972	2,303	108	101	3,484	5
	B	907	2,550	111	72	3,640	3
	C	413	5,354	218	19	6,004	3
1960	A	1,579	1,448	198	34	3,259	7
	B	1,692	1,564	189	36	3,481	5
	C	263	2,394	296	34	2,987	6

* February
B $r_s = 0.85$
C $r_s = 0.90$

to biomass estimation is solely a function of the variability these biases cause with respect to year-to-year differences between the capture and retention of sardine and anchovy larvae. For example, in Figure 5 the product moment regression coefficients, r for sardine egg or larval census estimate versus sardine biomass are plotted by total eggs, total larvae (1951-59), total larvae with outlyer censored (1953-59), and each larval size interval through 15.75 mm. All the coefficients are high and positive with pronounced minima at the egg stage and at the 9.75 mm stage. One might ascribe the minimum associated with eggs to the effect of "patchy" distribution on precision of estimate. I have no ready explanation of the 9.75 mm minimum or the 12.75 mm maximum which follows it.

Sette and Ahlstrom (1948, p. 521) discussed the concept of "area of station" relative to sardine eggs. Trial calculations of the same kind suggest that with respect to sardine larvae, assigning equal areas to stations is also close to the more exact method of erecting perpendicular bisectors to each nearest station and using the area of the polygon so formed. For anchovy larvae, however, there may be an important problem. To study this problem, the southern California inshore region was divided into "nearshore", i.e., the standard station closest to shore on each line, and "nearshore-excluded" segments. In the 40 quarters of the years 1951-60, the mean concentration of eggs per positive station in the "nearshore" region exceeded that of the "nearshore-excluded" section by 35%. Similarly the

proportion of positive stations was 87% "nearshore" and 68% in the "nearshore-excluded" region with respect to anchovy larvae.

In Table 7 I have compared the annual estimates of anchovy larvae using the quarterly regional census estimate of the entire region with the same estimate using the sum of the nearshore and nearshore-excluded segments of the region. The latter estimate is 8% lower than the regional census estimate, but it is not likely to be a bias since of the 10 annual estimates, the single estimate exceeds the partitioned estimate 5 times while the reverse is true an equal number of times. The Spearman rank coefficient of correlation is 0.85. Also, a comparison of the annual estimates from 1951 to 1959 regional census estimates and those from a census estimate by Ahlstrom (1967, Table 2) shows a Spearman rank correlation coefficient of 1.00. Thus, we may conclude that errors of the kind involving nearshore gradients in the incidence and intensity of anchovy spawning and larval survival, while important for some applications, do not measurably affect the regional census estimates.

One may reasonably ask whether estimates generated from monthly cruises are comparable to larval abundance estimates from a single cruise in each quarter. In Table 7 I have compared the annual estimates of anchovy larvae using all regular occupied stations within the quarter and a similar estimate using only January, April, July, and October, with February used in 1957 because the January cruise was incomplete. The Spearman rank coefficient for the comparison is 0.90: the mean value of the estimates from monthly cruises is 10% below the estimates from one cruise per quarter but in 5 years the monthly derived estimates exceed the quarterly and in 5 years the reverse is true. Thus, I conclude that differences which may arise from comparing estimates from quarterly and monthly cruises are not large enough to affect this study.

Technical errors should be relatively small and affect the catches of sardine and anchovy similarly. For example, the factor a_i, the area of mouth of the net is usually known to within 5%, the factor b_i is modified by the flow through the mouth of the net so that the length of tow is

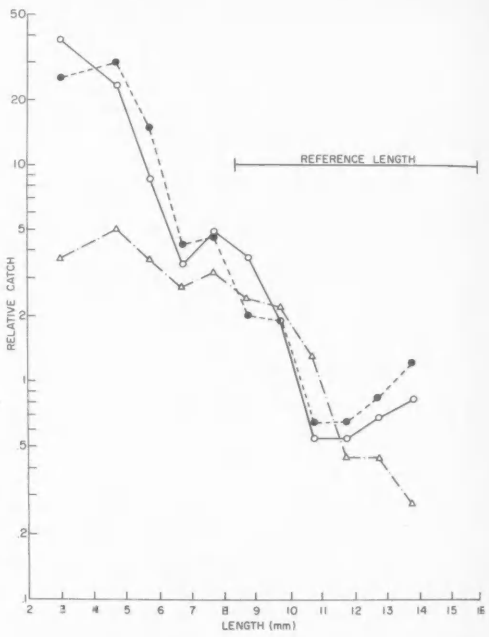

FIGURE 6.—The size frequency of sardine larvae captured in 1951-60 in the southern California inshore (clear dot, solid line), offshore (black dot, small dash), and seaward (triangle, large dash) regions. The size frequency effect is attributed to offshore transport (see text).

underestimated by 13-15%: an error as great as 5-10% results from the flowmeter being centered in the backwash of the bridle apex hardware (Smith and Clutter, 1965; Tranter and Smith, 1968; Mahnken and Jossi, 1967).

Two biases, which have yet to be evaluated, are likely to be important. In cold water, the larvae may tend to grow more slowly. Thus the regional census estimate for a cold quarter or cold year could prolong the period for which the larvae are vulnerable to sampling. Similarly, larvae may persist without food for extended periods yielding the same kind of error mentioned for temperature. No estimate has been made for either bias for anchovy or sardine larvae.

All the sardine and anchovy larvae collected by the CalCOFI net have been subjected to trans-

port with the wind-driven layer of the ocean (Sette, 1943). While the entire problem of transport is beyond the scope of this paper, a comparison of size frequencies of larvae in the southern California inshore, offshore, and seaward regions shows a disproportionately lower number of younger larvae in samples from farther offshore (Figures 6 and 7). The most likely explanation of these data is that older larvae transported to the offshore regions are present in excess of the numbers that have been spawned and hatched there. Further, this implies that the larva size frequency slope in the spawning area is biased for the same reason. If the usual sampling grid encloses the spawning area and the areas to which larvae are transported no overall bias should ensue.

The MacGregor estimate of anchovy and sardine biomass cited above, mentioned specific numbers of spawnings per year and sex ratios. Neither of these has been suitably evaluated as yet. At present, there is no way of calculating the number of batches spawned per year. In this paper, I assume that the anchovy is twice as fecund as sardine. An attempt will be made to evaluate the sensitivity to multiple spawning by proposing three spawning models, below. The sex ratio is presently derived from the fishery which is conducted over a very small proportion of the anchovy range. Since males are somewhat smaller, they may be expected to be recruited to the fishery somewhat later than females. In this report, the simple assumption of equality of biomass will be maintained. This will tend to overestimate the adult biomass by the degree in which the male biomass is overestimated.

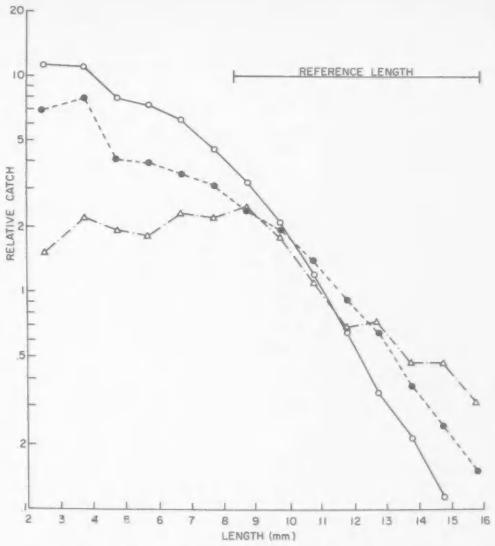

FIGURE 7.—The size frequency of anchovy larvae captured in 1951-60 in the southern California inshore (clear dot, solid line), offshore (black dot, small dash), and seaward (triangle, large dash) regions. The size frequency effect is attributed to offshore transport (see text).

TABLE 8.—Sample size frequency distribution for sardine and anchovy. Total larvae per 10 m^2 sea surface.

Mid-range x	Sardine f	fx	$fx/\Sigma fx$	Cumulative percent	Anchovy f	fx	$fx/\Sigma fx$	Cumulative percent
0.7	4	2.8	0.000	0.0	4	2.8	0.000	0.0
1.4	51	71.4	0.000	0.1	79	110.6	0.000	0.0
2.8	453	1,268.4	0.009	0.9	886	2,480.8	0.002	0.2
5.6	320	1,792.0	0.012	2.2	707	3,959.2	0.003	0.4
11.2	312	3,494.4	0.024	4.6	814	9,116.8	0.006	1.0
22.4	289	6,473.6	0.045	9.1	789	17,673.6	0.012	2.2
44.7	257	11,487.9	0.079	17.0	752	33,614.4	0.022	4.4
89.1	179	15,948.9	0.110	28.0	725	64,597.5	0.043	8.7
177.8	127	22,580.6	0.156	43.7	618	109,880.4	0.072	15.9
354.8	78	27,674.4	0.191	62.8	579	205,429.2	0.135	29.4
707.9	44	31,147.6	0.216	84.4	369	261,215.1	0.172	46.6
1,412.5	14	19,775.0	0.137	98.0	247	348,887.5	0.230	69.6
2,818.4	1	2,818.4	0.019	100.0	94	264,929.6	0.174	87.1
5,623.4					23	129,338.2	0.085	95.6
11,220.2					4	44,880.8	0.030	98.5
22,387.2					1	22,387.2	0.015	100.0
N	2,129				6,691			
$\bar{X}$	67.88				226.95			
Σfx		144,535.4				1,518,503.7		

TABLE 9.—Regional census estimates of total anchovy larvae (0-: no sampling).

Year	Quarter	Regions[1]											
		CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1940	1	0–	0–	771	196	0–	0–	0–	0–	0–	0–	0–	967
	2	0–	0–	258	214	0–	0–	0–	0–	0–	0–	0–	472
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1941	1	0–	0–	184	351	0–	0–	0–	0–	0–	0–	0–	535
	2	0–	0–	422	579	0–	0–	0–	0–	0–	0–	0–	1,001
	3	0–	0–	27	8	0–	0–	0–	0–	0–	0–	0–	35
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1950	1	0	0	10	9	4	43	17	1	13	5	0	102
	2	0	0	232	319	27	115	23	0	152	13	0	881
	3	994	265	338	5	2	9	1	0	2	3	0	1,619
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1951	1	5	0	135	8	0	289	17	150	2,537	147	1	3,289
	2	4	6	609	24	5	203	66	78	289	179	80	1,543
	3	25	53	111	21	0	454	0	0	49	57	0	770
	4	18	0	540	21	0	266	2	0	55	0	0	902
1952	1	0–	0–	87	33	0	1,372	111	0	1,762	40	0	3,405
	2	0	0	261	7	1	732	32	0	1,665	145	0	2,843
	3	7	69	314	16	3	462	1	2	240	12	2	1,128
	4	0	0	134	23	0	558	31	0	8	2	0	756
1953	1	0–	0–	578	67	6	1,649	247	2	4,160	78	227	7,014
	2	0	0	184	17	0	535	85	2	424	238	14	1,499
	3	2	0	763	38	7	373	2	0	150	33	0	1,368
	4	0–	0–	1,904	882	0	831	48	0	84	2	0	3,751
1954	1	654	0–	3,123	723	6	1,090	97	6	4,116	474	615	10,904
	2	1	0	516	98	2	878	28	3	1,872	498	350	4,246
	3	451	0	519	307	426	182	0	0	231	191	0	2,307
	4	58	0–	237	73	11	234	153	0	301	9	0	1,076
1955	1	0–	0–	2,012	283	6	7,152	499	11	750	312	2	11,027
	2	2	0	1,074	246	6	540	266	296	787	380	24	3,621
	3	7	0	849	184	35	257	3	0	602	9	27	1,973
	4	5	10	150	19	0	210	15	0	59	7	4	479
1956	1	0–	0–	236	203	46	1,140	832	409	1,786	1,107	2	5,761
	2	0	0	1,166	63	14	2,239	37	1	1,737	154	2	5,413
	3	247	0	708	562	21	1,413	0	0	807	8	0	3,766
	4	0–	0–	156	115	4	0–	0–	0–	0–	0–	0–	275
1957	1	0–	0–	3,314	1,085	969	2,720	102	3	2,683	69	0	10,945
	2	20	21	3,601	814	69	853	104	8	426	44	13	5,973
	3	5	20	791	592	64	380	1	0	358	234	17	2,462
	4	64	0	267	229	4	86	0	0	10	0	0	660
1958	1	1,620	1,227	2,316	2,407	268	4,680	618	16	4,606	788	5	18,551
	2	252	15	2,912	1,168	497	1,099	384	2	165	57	44	6,590
	3	413	387	403	1,508	84	143	5	0	15	0	0	2,958
	4	11	5	68	34	0	54	2	0	4	0	0	173
1959	1	1,722	0	972	4,452	654	701	51	1	1,595	51	0	10,199
	2	1,101	318	2,303	3,074	498	3,227	651	1	464	453	0	12,090
	3	232	128	108	242	33	62	1	1	197	9	0	1,033
	4	5	0	101	2	0	9	4	0	20	0	0	141
1960	1	185	0	1,579	1,393	279	4,647	1,697	592	6,821	2,327	686	20,206
	2	127	64	1,448	2,694	1,065	2,679	626	259	582	472	11	10,027
	3	155	105	198	70	22	106	69	6	294	7	0	1,032
	4	1	0	34	9	0	67	0	0	21	2	15	149
1961	1	7	0	144	45	0	2,145	143	0	13,436	234	0	16,154
	2	10	0	1,513	955	2,258	2,186	516	215	3,068	1,683	115	12,519
	3	677	310	359	1,127	1,070	114	1	0	27	9	0	3,694
	4	35	15	18	25	4	32	3	2	30	7	0	171
1962	1	56	0	2,285	825	3	2,413	1,021	24	12,570	2,248	0	21,445
	2	877	0	6,555	5,953	5,900	15,483	1,516	228	1,208	1,631	186	39,537
	3	0–	0–	1,214	120	40	505	4	5	162	92	0	2,142
	4	41	5	134	65	8	124	1	0	256	0	0	634

TABLE 9.—Continued.

Year	Quarter	Regions[1]											
		CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1963	1	7	0	7,543	1,481	73	8,088	5,446	688	8,730	381	184	32,621
	2	1,395	175	3,291	6,132	12,821	1,810	389	42	507	182	86	26,830
	3	0–	0–	180	649	133	187	8	8	305	21	7	1,498
	4	0–	0–	279	161	2	92	3	2	45	0	0	584
1964	1	1,420	0	4,137	3,552	7,213	2,895	133	66	6,678	148	5	26,247
	2	3,056	82	4,524	6,223	3,656	1,063	1	0	384	73	77	19,139
	3	538	125	353	1,814	1,516	1,058	26	15	204	6	0	5,655
	4	0–	0–	945	110	3	71	0	2	81	0	0	1,212
1965	1	16	0	10,145	3,803	669	6,158	1,136	1,013	7,171	396	5	30,512
	2	1,160	0	6,870	7,561	6,219	2,257	424	1,112	6,205	91	17	31,916
	3	75	5	6,304	3,130	3,042	1,056	286	4	866	5	0	14,773
	4	0–	0–	1,037	733	121	185	0	0	15	0	0–	2,091
1966	1	2,973	0	7,078	4,285	409	4,426	275	9	3,289	189	15	22,948
	2	181	0	7,823	9,902	1,164	1,065	63	5	1,023	2	0	21,228
	3	738	56	2,427	960	214	881	36	2	454	90	0	5,858
	4	51	2	1,022	62	14	181	4	0	830	0	0	2,166
1967	1	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	2	0–	0–	5,646	2,565	367	1,901	59	0	618	23	0	11,179
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0
	4	0–	0–	0–	0–	0–	966	155	8	224	605	0	1,958
1968	1	458	0	3,318	3,259	406	2,342	1,851	0	0–	0–	0–	11,634
	2	4	0	4,020	1,194	697	960	397	0	303	361	0	7,936
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1969	1	919	0	16,404	11,163	1,028	5,712	1,671	5	4,198	588	38	41,726
	2	3	0	5,982	2,364	294	3,459	350	196	612	237	3	13,500
	3	28	91	3,101	678	92	282	13	19	178	13	0	4,495

[1] CCI = Central California inshore
CCO = Central California offshore
SCI = Southern California inshore
SCO = Southern California offshore
SCS = Southern California seaward
BCI = Baja California inshore
BCO = Baja California offshore
BCS = Baja California seaward
SBI = South Baja inshore
SBO = South Baja offshore
SBS = South Baja seaward

The anchovy spawns over a small portion of its range apparently while still schooled; it also spawns over a small portion of the day (25%); it now appears that most spawning takes place just after the full moon, ca. 20% of the lunar month (Smith).[4] In addition, the spawning behavior is highly seasonal with most spawning occurring in the first half-year. Biases result from sampling during a period in which spawning is occurring (Sette and Ahlstrom, 1948, p. 520), and similar errors may result from missing or oversampling spawning peak periods or dense small patches. Although patches would tend to disperse toward randomness, this process appears to be very slow relative to the duration of the larval stage. Patchiness persists and may be augmented by predation. For this reason, the samples have been pooled to reduce variance wherever possible. Nevertheless, sample sizes range from zero to tens of thousands of larvae, and a pooled summary may still be based on a chance large sample. In all cases, the above error analysis was done with a sample frequency plot in view and all "outlyers" were examined for effect on the sampling question. All samples taken between 1951 and 1960 are listed by frequency distribution in Table 8 for sardine and anchovy total larvae.

Anchovy larvae abundance (Table 9) and sardine larvae abundance (Table 10) for 11 regions and the years 1940, 1941, 1949-69, are listed for each region and quarter in which sampling took place at standard stations. Figure 8 shows the comparison of the regional census estimates and standard haul summations from 1951 to 1966 (Ahlstrom, 1968). The close agree-

[4] Smith, P. E. Lunar periodicity in the spawning of the northern anchovy (*Engraulis mordax*). Unpublished manuscript filed at National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92037.

TABLE 10.—Regional census estimates of total sardine larvae (0-: no sampling).

Year	Quarter	Regions[1]											
		CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1940	1	0–	0–	81	343	0–	0–	0–	0–	0–	0–	0–	424
	2	0–	0–	141	210	0–	0–	0–	0–	0–	0–	0–	351
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1941	1	0–	0–	154	211	0–	0–	0–	0–	0–	0–	0–	365
	2	0–	0–	277	313	0–	0–	0–	0–	0–	0–	0–	590
	3	0–	0–	1	5	0–	0–	0–	0–	0–	0–	0–	6
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1949	1	0	0	0	0	0	9	2	0	0–	20	3	34
	2	0	0	2	11	14	259	1	1	300	2	3	593
	3	304	7	5	12	5	0	0	0	0	0	1	334
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1950	1	0	0	0	0	0	92	1	0	117	128	2	340
	2	0	2	116	206	128	60	91	3	1,951	402	0	2,959
	3	9	4	3	2	2	1	2	0	10	11	0	44
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1951	1	0	0	3	0	0	19	4	0	235	63	0	324
	2	0	0	3	89	18	101	103	8	1,313	107	17	1,759
	3	0	0	4	1	0	270	0	0	94	7	0	376
	4	0	0	0	0	0	146	0	0	79	1	0	226
1952	1	0–	0–	1	5	0	117	90	0	464	87	2	766
	2	0	0	27	51	1	95	194	0	427	731	0	1,526
	3	0	0	8	39	0	49	12	0	168	5	0	281
	4	0	0	0	0	0	37	0	0	19	4	0	60
1953	1	0–	0–	0	0	0	48	199	0	342	94	40	723
	2	0	0	1	0	0	73	509	0	123	370	4	1,080
	3	0	0	1	0	0	86	0	0	100	22	0	209
	4	0–	0–	0	0	0	62	0	0	113	2	0	177
1954	1	0	0–	0	1	0	20	185	93	681	51	110	1,141
	2	1	0	80	320	204	355	63	37	290	140	9	1,499
	3	0	0	4	0	0	59	2	0	166	75	0	306
	4	0	0–	0	0	0	5	0	0	239	3	0	247
1955	1	0–	0–	1	2	8	179	278	285	142	110	0	1,005
	2	0	0	35	146	85	72	99	70	14	8	0	529
	3	0	0	1	31	34	228	4	0	34	9	0	341
	4	0	0	0	0	0	18	0	0	64	2	0	84
1956	1	0–	0–	0	0	0	71	58	33	330	54	0	546
	2	0	0	2	173	48	52	11	14	70	93	0	463
	3	0	0	2	43	9	307	0	0	335	0	0	696
	4	0–	0–	1	0	0	0–	0–	0–	0–	0–	0–	1
1957	1	0–	0–	0	0	0	177	1	2	144	12	0	336
	2	0	0	3	188	4	19	3	1	1	0	0	219
	3	0	20	15	0	0	303	0	0	108	0	0	446
	4	0	0	0	38	0	80	0	0	15	3	0	136
1958	1	0	0	83	52	0	259	0	0	224	21	0	639
	2	3	0	52	27	4	9	2	0	12	1	67	177
	3	0	0	26	94	2	287	1	0	217	0	0	627
	4	0	0	0	0	0	9	0	0	1	0	0	10
1959	1	0	0	74	15	3	24	0	0	35	5	0	156
	2	0	0	33	31	1	15	0	0	19	1	0	100
	3	2	0	2	44	0	82	0	0	78	0	0	208
	4	0	0	19	0	0	67	0	0	20	0	0	106
1960	1	0	0	33	13	0	6	0	0	207	0	0	259
	2	0	0	40	7	0	2	0	0	6	0	0	55
	3	0	0	13	0	0	228	81	0	121	2	0	445
	4	0	0	1	0	0	138	0	5	72	0	0	216
1961	1	0	0	0	29	0	1	0	0	54	0	0	84
	2	0	0	7	4	6	0	8	0	73	0	0	98
	3	0	0	14	2	0	90	0	0	17	0	0	123
	4	0	0	15	0	0	8	0	0	295	19	0	337

TABLE 10.—Continued.

Year	Quarter	Regions[1]											
		CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1962	1	0	0	10	0	0	1	0	0	204	0	0	215
	2	0	0	7	7	0	18	0	0	9	2	0	43
	3	0–	0–	26	1	0	240	0	0	56	23	0	346
	4	0	0	1	1	0	14	0	0	109	2	0	127
1963	1	0	0	50	0	0	62	0	0	3	0	0	115
	2	3	0	1	0	0	0	3	0	10	0	0	17
	3	0–	0–	1	0	3	54	0	0	49	0	0	107
	4	0–	0–	7	5	0	96	1	0	31	0	0	140
1964	1	0	0	1	0	0	0	0	0	229	0	0	230
	2	0	0	0	0	0	0	0	0	9	1	0	10
	3	0	0	4	0	0	22	0	0	159	0	0	185
	4	0–	0–	19	0	0	3	0	0	58	0	0	80
1965	1	0	0	2	0	0	5	0	0	7	0	0	14
	2	1	15	0	0	0	3	0	0	0	0	0	19
	3	0	0	7	0	0	4	0	0	429	1	0	441
	4	0–	0–	1	0	0	406	0	0	216	1	0–	624
1966	1	3	0	1	0	0	19	0	0	49	0	0	72
	2	0	0	10	0	0	1	0	0	2	0	0	13
	3	0	0	1	0	0	50	4	0	262	1	0	318
	4	0	0	1	0	0	238	4	0	87	2	0	332
1967	1	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	2	0–	0–	5	0	0	105	0	0	1,111	0	0	1,221
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	11	0	0	59	0	0	70
1968	1	0	0	0	0	0	0	0	0	0–	0–	0–	0
	2	0	0	2	0	0	5	1	0	0	0	0	8
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1969	1	1	0	1	1	0	5	1	0	0	0	0	9
	2	0	0	3	0	0	10	3	0	30	0	0	46
	3	0	0	1	0	0	48	0	0	25	3	0	77

[1] CCI = Central California inshore
CCO = Central California offshore
SCI = Southern California inshore
SCO = Southern California offshore
SCS = Southern California seaward
BCI = Baja California inshore
BCO = Baja California offshore
BCS = Baja California seaward
SBI = South Baja inshore
SBO = South Baja offshore
SBS = South Baja seaward

ment between these values lends support to the idea that the method of data assembly causes little bias relative to size of the major fluctuations in anchovy larva abundance. Both the Spearman rank difference and the product-moment correlation coefficients are 0.99.

MacGregor (1968) suggested that the problem of determining the number of batches of eggs spawned per year per female is the major source of imprecision and bias in the adult biomass estimates from egg census and fecundity data. He further suggested that the best strategy for egg census would be to conduct an intensive cruise over a brief period in which no female is likely to spawn more than once. For the purpose of this paper, a preliminary judgment as to the importance of multiple spawnings in the larva ratio estimate of anchovy biomass may be made by comparing three models of spawning behavior. The first model is that the adult biomass is proportional to the regional census estimate. This model assumes that the product of the number of eggs spawned per ton of female, the number of spawnings per year, and the mortality rate of the larvae is stable. The second model is that each anchovy spawns once in the winter quarter. The third model is that each anchovy spawns in the single maximum quarter. Restated, the adult biomass is proportional to the 1) annual average regional census estimate of larval abundance, 2) winter quarter regional census estimate, or 3) annual maximum quarterly regional census estimate. The 1951-66 data for the Ahlstrom standard haul summation, the

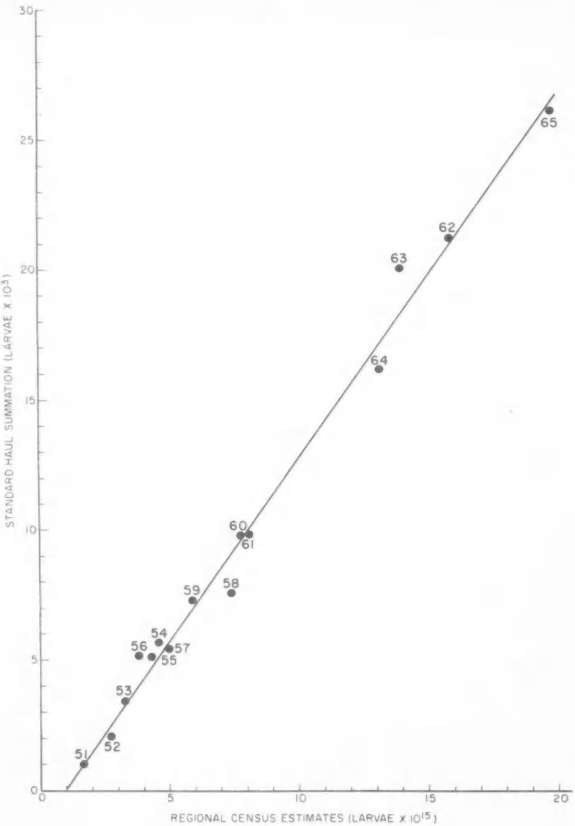

FIGURE 8.—A 16-year comparison of the regional census estimate derived for this paper and the standard haul summation quarterly average (Ahlstrom, 1968).

average regional census estimate, the winter spawning, and seasonal maximum are found in Figure 9. It is clear that the same trend and magnitude of increase are seen from each model. Since there is no obvious difference, the annual average regional census estimate of larva abundance will be used for the current biomass estimates.

It may be seen from Table 9 that the anchovy larvae have increased in number, particularly in the southern California section. Figure 10 illustrates the subdivision of the regional census estimate annual totals by section of the coast from 1951 to 1966. Within the southern California section, the inshore region was the dominant producer of anchovy larvae for the first 7 years. In the next 3 years, the southern California offshore became equally important in numbers of anchovy larvae. Between 1962 and 1965, the seaward region (160-280 miles off the coast) was a very important locality for anchovy larvae and this influence dropped radically to pre-1961 values in 1966 (Figure 11). This change and a smaller one inshore resulted in an appreciable lowering of the overall total in 1966 (Figure 10). The subpopulations of the northern anchovy have been assigned to coastal sections (Vrooman[5]; Vrooman and Smith, 1972),

[5] Vrooman, A. M. Anchovy subpopulations. Unpublished manuscript filed at National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92037.

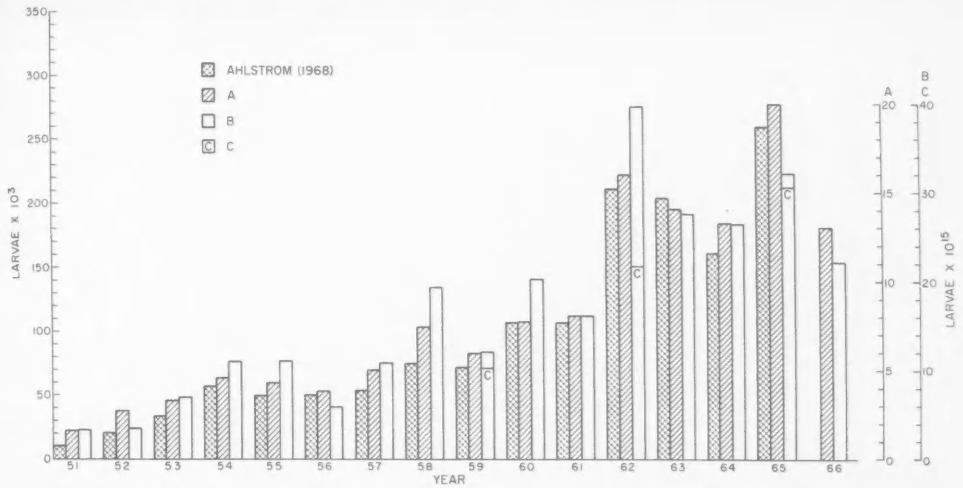

FIGURE 9.—A time-series comparison of the annual quarterly average standard haul summation (Ahlstrom, 1968, double cross-hatch) and the annual quarterly average regional census estimate ("C", clear bar including line C if any).

and the major portion of increase of northern anchovy is ascribed to the "central" subpopulation which spawns off southern California.

The seasonal contribution of anchovy larva abundance from 1951 to 1966 is illustrated in Figure 12. From 1951 through 1959, winter-caught larvae dominated the total. Beginning in 1960, spring larva abundance became increasingly important and, in 1962, substantially exceeded winter larva abundance. As mentioned above, the changing day-length in the spring quarter makes an appreciable difference for which the data have not yet been corrected. The spring-caught larvae are underestimated as a result. No correction has been applied for temperature- or food-specific growth rate changes, by season.

The increase of numbers of anchovy larvae shown in the foregoing regional census estimates could result from the traditional spawning areas being more completely covered with larvae, from new spawning areas being covered, or there being more larvae per unit area. There are instances of all three in the 1951-66 period. In particular, in the southern California section of the coast, where most of the increase took place, the primary effect has been the additional covering of traditional spawning areas. For example, in the southern California offshore region, April through June, 7 of 50 tows contained anchovy larvae in 1953, 25 of 48 tows contained larvae in 1955, and 51 of 53 tows had anchovy larvae in 1959 (14.0%, 52.1%, and 96.2% respectively). If one fits a regression line to the increasing proportions of positive stations with respect to anchovy larvae off southern California the slopes in percent per year from 1952 to 1966 follow:

	Winter	*Spring*	*Summer*	*Fall*
Inshore (0-80 miles)	1	2	1	1
Offshore (80-160 miles)	4	6	4	1
Seaward (160-280 miles)	2	7	2	1

Also, there are more anchovy larvae per positive station than before. In the years 1962-66 there are 5-8 times as many larvae per positive station as in 1951 (Table 11). The number of larvae per positive station is not independent of the proportion of positive stations. One interpretation of samples of larvae is that they are drawn from relatively small (100's of meters, Smith, in press) patches of larvae which are dispersing in such a way that they tend to overlap. For example, for randomly distributed

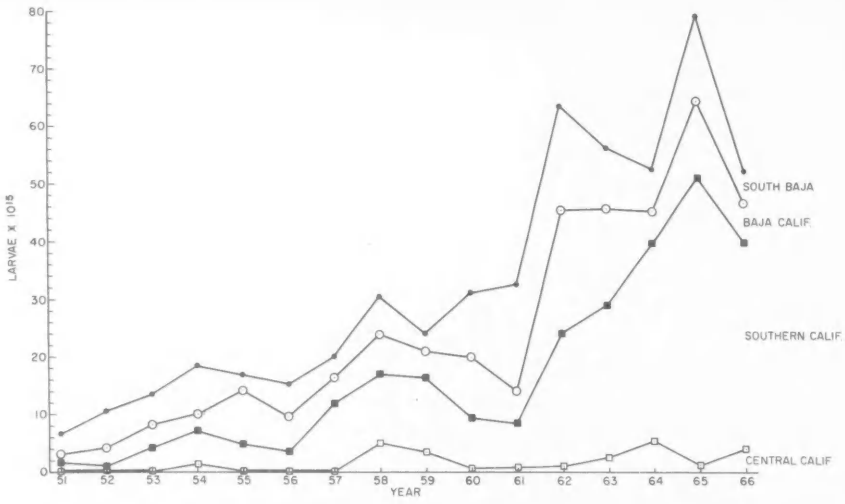

FIGURE 10.—A time-series comparison of the annual total regional census estimates of anchovy larvae as grouped by coastal section. The highest line (solid circle) is comparable to the quarterly average of "A" in Figure 9. The space between the top line and the line with open dots represents the contribution to the total by stations in the south Baja section. The space between the open dot line and the line connecting the solid squares represents the contribution of the Baja California section to the total. The space between the line connecting solid squares and the line connecting open squares represents the contribution of the southern California section. The space between the lines connecting open squares and the abscissa represents the contribution of the central California section to the total. For relative areas of the sections refer to Table 3 and Figure 2.

patches covering 0.1 of the area, the chance of encountering two patches is 0.01; with patches covering 0.9 of the area, the chance of encountering two patches simultaneously is roughly 0.8. In the southern California inshore and offshore regions, the proportion of positive stations is related to the number of larvae per positive station in the following way:

$$\log_{10} N_1 = 3.20\,P_1 - 0.218 \quad t = 11.17 \quad 37\text{ df}$$
$$\log_{10} N_2 = 2.13\,P_2 + 0.748 \quad t = 9.95 \quad 37\text{ df}$$
$$\log_{10} N_3 = 2.32\,P_3 + 0.573 \quad t = 14.40 \quad 76\text{ df}$$

where N_i = number of larvae per 10 m² per positive station in the ith region, when $i = 1$ = southern California inshore region, when $i = 2$ = southern California offshore region, when $i = 3$ the inshore and offshore regions are combined;

P_i = proportion of positive stations in winter and spring in offshore ($i = 2$) or inshore areas ($i = 1$), or both ($i = 3$).

If the patchy model applies, this set of equations is good only for the CalCOFI standard tow, in these two regions. For example on theoretical grounds, if the standard tow were to sample under 20 m² rather than the average 3 m² as at present, one would expect the proportion of positive tows to rise and the number per positive tow to decrease for any given average of anchovy larvae per total unit area.

In addition to an increasing proportion of positive tows in traditional spawning areas and increasing numbers of larvae per positive tow, the southern California seaward region is an example of a new spawning area being invaded in

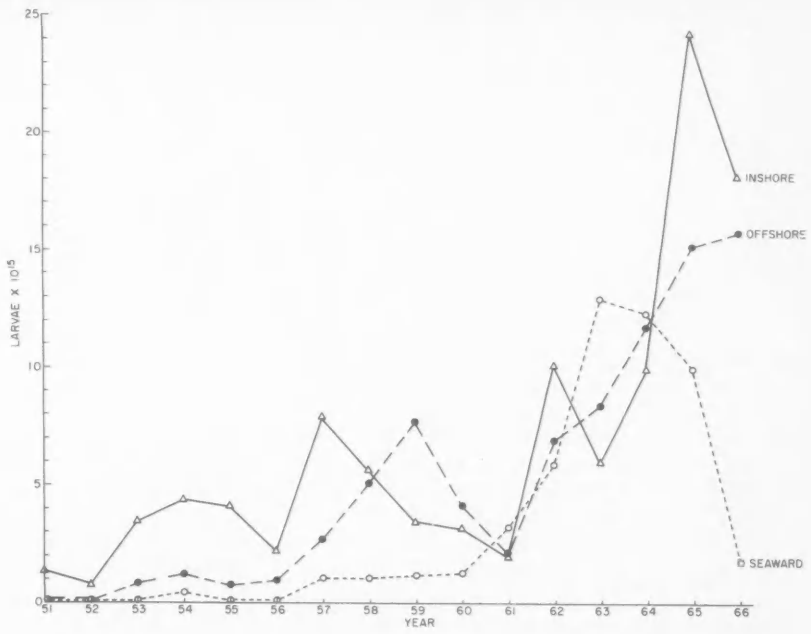

FIGURE 11.—A time-series comparison of the annual total regional census estimates of anchovy larvae as grouped by distance from shore within the southern California section. Lines connecting open triangles represent the southern California inshore, closed circles, the southern California offshore, and open circles, the southern California seaward. For relative areas of the regions refer to Table 3 and Figure 2.

the early sixties and becoming largely unused by the mid-1960's. The incidence of larvae has continued at less than 10% of the 1962 peak year in the southern California seaward region (Table 9).

THE CURRENT ESTIMATE OF ANCHOVY SPAWNING BIOMASS

The practice adopted in this paper for estimating anchovy spawning biomass consists of 1) regression estimates of the relationship between sardine larval abundance and Murphy's estimate (1966) of sardine biomass; 2) the ratio of anchovy:sardine larva abundance until 1958; 3) the regression estimate of the relationship between anchovy larva abundance between 1951 and 1958 and the sardine-derived anchovy biomass; and 4) the use of regression estimates to calculate anchovy and sardine biomass estimates outside the regression period. This differs from Murphy's (1966) method of using an anchovy:sardine ratio for each anchovy estimate. It also differs from Ahlstrom's (1968) method of tying each estimate to the biomass of sardine adults in 1958. Since regressions between two variables with time trends are influenced by the degree of temporal coherence of each variable, caution is warranted in their use. Confidence intervals may be calculated but their meaning is not clear due to the violation of the assumption of independence among the values used to calculate the regression. The regression estimates are used here as a simple shorthand method of reporting an apparent relationship.

The spawner biomass estimates of anchovy and sardine which result from this and previous

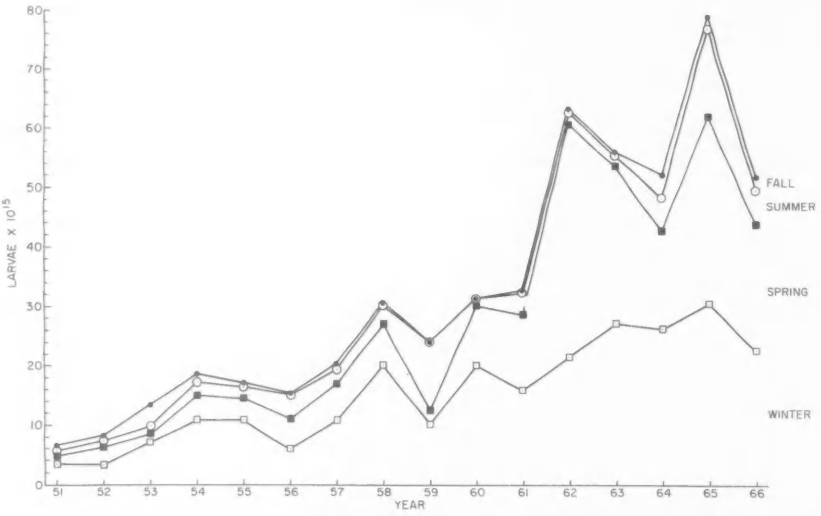

FIGURE 12.—A time-series comparison of the annual total regional census estimates of anchovy larvae as grouped by season of spawning. The highest line (solid circle) is comparable to that found in Figure 10 and to the height of "A" in Figure 9.

studies are found in Table 12. The primary objective of this study concerns the period of increase from 1951 to 1966. Despite various technical deficiencies in the basic data, the years 1940, 1941, 1950, and 1969 are also estimated in the section to follow.

The first column of Table 12, Murphy's (1966) sardine spawner biomass estimates, is reproduced without change. If those estimates are changed by later studies, all other values in the table must be adjusted. The important features of Table 12 are 1) a regression estimate to derive sardine spawner biomass estimates from the regional census estimates of total sardine larvae; 2) a ratio estimate of anchovy spawner biomass which is half the product of the anchovy:sardine ratio and the sardine biomass; and 3) a regression estimate of anchovy spawner biomass derived from the regional census estimate of total anchovy larvae.

The equation for a least squares estimate of sardine spawner biomass and sardine total larvae derived for this study is:

$$B_s = 0.230L_s - 0.057$$

where B_s is the annual estimate of sardine spawner biomass in thousands of short tons and L_s is the regional census estimate annual total of sardine larvae in numbers times 10^{12} in the years 1951-58, excluding 1953. The years 1953 and 1959 were eliminated as outlyers on a scatter diagram when it was found that the assumption of constant size distribution of larvae had been violated. The equation was later simplified by assuming a zero intercept to:

$$B_s = 0.206L_s$$

The anchovy spawner biomass estimates were derived from the ratio of anchovy:sardine larvae and the Murphy sardine biomass estimate in the following way:

$$B_a = c\left(\frac{L_a}{L_s}\ B_s\right)$$

where B_a is the ratio estimate of anchovy spawner biomass, L_a is the regional census estimate

TABLE 11.—Anchovy larvae per positive station.

Year	No. of positive stations	No. of anchovy larvae	No. of larvae per positive station
1951	344	26,951	78
1952	399	53,457	134
1953	539	85,178	158
1954	626	126,191	202
1955	558	134,017	240
1956	482	104,192	216
1957	518	135,966	262
1958	667	197,082	295
1959	729	182,176	250
1960	628	254,263	405
1961	420	88,925	258
1962	374	190,735	510
1963	370	172,611	466
1964	372	141,498	380
1965	392	234,850	599
1966	738	364,689	494

of anchovy total larvae, and c is a constant representing the relative fecundity of sardine relative to anchovy, here assumed to be approximately 0.5. Lenarz (1972) suggests a constant of escapement of 1.1 to counteract the tendency for anchovy larvae to pass through the mesh openings of the standard silk net to a greater extent than sardine larvae. This experimentally derived estimate from paired tows which captured both species in standard and fine mesh nets is considered too small to be appreciable on the scale of variability encountered in plankton tows. Murphy's (1966) estimate of the escapement factor, i.e., 2, is rejected.

The equation for a least squares estimate of the anchovy spawner biomass and anchovy total larvae is:

$$B_a = 0.094\, L_a + 0.072$$

defined in the same way as the sardine case above. Similarly, the zero intercept was forced, giving:

$$B_a = 0.098 L_a$$

which is the equation used for the regression estimate of anchovy spawner biomass.

The aberrant years 1953 and 1959 were recalculated assuming the slope and the Murphy sardine spawner biomass estimate are correct and that the sardine larva estimates are biased or imprecise. The recalculated estimates (parentheses, Table 12) appear to conform better to the trends of anchovy biomass and anchovy-sardine ratio.

The data from 1940, 1941, 1950, and 1969 have been manipulated to extend the biomass estimates. The 1940 and 1941 cruises were

TABLE 12.—Sardine and anchovy spawner biomass estimates by ratio and regression methods.

	Murphy sardine spawner biomass ($\times 10^3$T)	Regression sardine spawner biomass ($\times 10^3$T)	Sardine larval estimate ($\times 10^{12}$)	Anchovy larval estimate ($\times 10^{12}$)	Anchovy sardine ratio	Ratio anchovy spawner biomass ($\times 10^3$T)	Regression anchovy spawner biomass ($\times 10^3$T)
1940	1,296		1,634*	5,943*	3.64	2,359	
1941	2,001		2,476*	7,104*	2.87	2,871	
. . .							
1950	716		3,343	2,602	0.78	279	
1951	570	553	2,685	6,504	2.42	690	637
1952	554	542	2,633	8,132	3.09	856	797
1953	709	450	2,189 (3,442)**	13,632	6.23 (3.96)**	2,209 (1,404)**	1,335
1954	668	658	3,193	18,533	5.80	1,937	1,816
1955	425	404	1,959	17,100	8.73	1,855	1,676
1956	293	351	1,706	15,215	8.92	1,307	1,491
1957	212	234	1,137	20,040	17.63	1,869	1,964
1958	281	299	1,453	28,272	19.46	2,875	2,771
1959	190	117	570 (922)**	23,463	41.16 (25.45)**	3,910 (2,418)**	2,299
1960		201	975	31,414	32.22		3,079
1961		132	642	32,538	50.68		3,189
1962		151	731	63,758	87.22		6,248
1963		78	379	61,533	162.36		6,030
1964		104	505	52,253	103.47		5,121
1965		226	1,098	79,292	72.21		7,771
1966		151	735				
. . .				52,200	71.02		5,116
1969		27†	132†	33,623†	254.72†		3,293†

* 1940, 1941—larval estimates seasonally adjusted.
** Parenthetic numbers for 1953 and 1959 assume larval numbers biased.
† 1969—larval counts 75% complete; adjusted for extra retention of small larvae.

conducted during the sardine spawning season, but excluded an important portion of the anchovy spawning season. Similarly, the cruises only sampled 20% of the area we now consider routinely surveyed. The ratio of sardine and anchovy larvae was used for 1950 and will not be discussed further. The 1969 samples systematically violated the assumption of stable size composition of larvae.

The cruises of 1940 and 1941 were conducted over the southern California inshore and offshore regions in the spring and summer. The total for both species in both regions and in both years was derived by simulation of analogous cruises within the 1951-60 survey period and the product-moment correlation coefficient is listed for each species, for each region, and year.

Year	*Species*	*Region*	*Original*	*Seasonally adjusted*	*Correlation coefficient*
1940	Anchovy	SCI	1,545	3,229	0.794
		SCO	820	2,714	0.945
		Total	2,365	5,943	
1940	Sardine	SCI	502	726	0.794
		SCO	891	908	0.955
		Total	1,393	1,634	
1941	Anchovy	SCI	1,494	3,257	0.845
		SCO	2,104	3,847	0.962
		Total	3,598	7,104	
1941	Sardine	SCI	987	1,305	0.807
		SCO	1,161	1,171	0.981
		Total	2,148	2,476	

The ratio of this group of samples, within the same boundaries as the other regional census estimates used here, change from 1.70 to 3.64 in 1940 and change from 1.68 to 2.87 in 1941. Accordingly, these ratios are used in Table 12.

The 1969 data point for anchovy is modified in a crude attempt to adjust for the extra retention of anchovy larvae in a new sampling net (see Figure 4) which retains approximately 50% more larvae. The 1969 surveys were conducted with a 1-m net with 50% more open area, more regular mesh apertures, and an average mesh width of 0.505 mm rather than the 0.55 mm aperture silk net (used and wet). The effect of additional mesh on reducing the extrusion effect of filtration pressure is discussed in Tranter and Smith (1968).

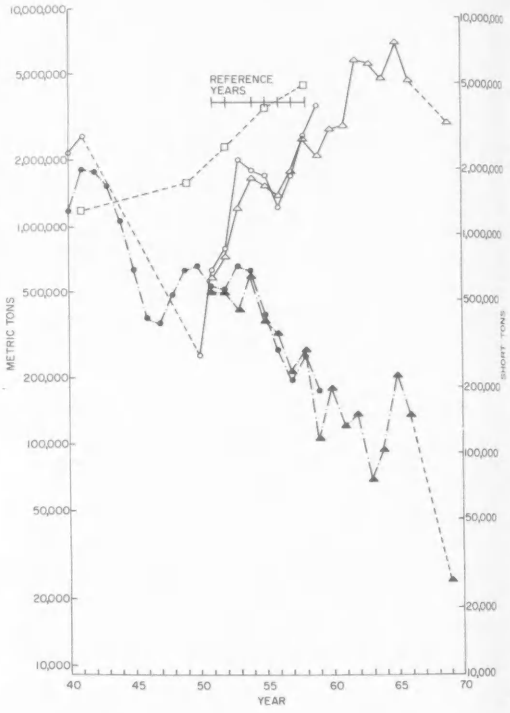

FIGURE 13.—A time-series comparison of sardine and anchovy biomass estimates from 1940 through 1969. The solid circle represents sardine biomass as calculated from the fishery by Murphy (1966) and extends from 1940 to 1959. The solid triangle represents sardine biomass derived from a regression estimate of the relationship between the Murphy biomass estimate and the annual total regional census estimate of sardine larvae during the reference years and is extended from 1951 through 1969. The open circle represents the estimates of biomass derived from the ratio of anchovy larvae to sardine larvae and the Murphy sardine biomass estimate from 1940 to 1959. The open triangle represents anchovy biomass derived from a regression estimate of the relationship between the anchovy tonnage calculated from the anchovy:sardine larvae ratio, and the annual total regional census estimate of anchovy larvae and extends from 1951 through 1969. The open squares represent the Murphy estimate of anchovy spawning biomass by 3-year averages (Murphy, 1966, Figure 17, p. 65). Dashed lines represent interpolations between nonadjacent years.

Figure 13 contains all the estimates resulting from this study. Murphy's sardine biomass estimates are plotted from 1940 to 1959. The anchovy biomass estimates derived from the anchovy sardine ratio and the anchovy larva regional census in 1940, 1941, and 1950 through 1959. The regression estimates are reproduced from 1951 to 1959 for comparison with the Murphy sardine biomass and ratio-derived anchovy biomass. The regression estimates of both sardine and anchovy spawner biomass are extended through 1966 and a tentative estimate for 1969 is placed for comparison.

DISCUSSION

Important changes in the size of the anchovy population have occurred in the California Current area over the past two decades. The increase of anchovy has coincided with the continuing decrease of sardine in the same area. All available evidence indicates that the anchovy and sardine populations declined between 1941 and 1951, and thereafter the anchovy underwent a sustained increase reaching a plateau of 5-8 million metric tons between 1962 and 1966. This population size may be between 2 and 3 times the anchovy spawning population of 1940-41 and between 5 and 10 times the anchovy population in 1950-51. Changes of this magnitude in the absence of a fishery underscore the importance of natural fluctuations in the population size of a fish species. Fishery management of such a species must be responsive to changes of this magnitude and rapidity.

Murphy (1966, 1967) speculated on the effect of the anchovy population on the recovery of the sardine population. Neither the feeding of anchovy and sardine nor the population dynamics of the food organisms is well enough understood in the California Current. Since the size frequency curves of larvae are relatively invariable (Ahlstrom, 1965; Lenarz, in press) one would expect competition, if any, to occur in the juveniles and pre-recruits of either species.

One interesting fact may be the decline of sardine spawning in the spring and summer has coincided with an increase of spawning in spring by the anchovy. In the estimates of spawner biomass of sardine and anchovy, no attention has been given the possibility that fecundity in numbers of eggs per batch and number of batches per unit time is plastic.

The numbers of anchovy and sardine larvae have been used here exclusively to describe changes in the adult biomass which spawned them. Since this process seems so effective, one might wonder what is required to refine techniques so that spawning, and larval and juvenile survival, may be used to predict the recruitment of year classes to the fishery. I believe the two major barriers are that 1) the size composition of the larvae of both species is so dependent on the sampling gear that mortality rates will remain too crude to project survival and 2) the effect of transport of larvae, particularly offshore to "unfavorable" areas, is neither well enough measured nor understood to effect predictive sampling systems.

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PRE-EXPLOITATION ABUNDANCE OF TUNAS IN THE EQUATORIAL CENTRAL PACIFIC

GARTH I. MURPHY[1] AND RICHARD S. SHOMURA[2]

ABSTRACT

The tuna resources and the environment in the equatorial central Pacific were investigated from 1950 to 1954. This report summarizes the data from these investigations and examines the distribution and relative abundance of tunas in relation to the environment.

The circulation of the waters of the equatorial region is described. The generally accepted view of a zonally oriented flow pattern of the South Equatorial Current between the equator and the Countercurrent is modified, and a model is proposed which regards the circulation as a series of homologous northwestward flowing cells. The evidence supporting this type of flow pattern is presented and discussed.

The variation in abundance of deep-swimming yellowfin tuna in space and in time is analyzed in relation to various environmental features. The hypothesis developed is that the change in abundance of yellowfin tuna is a function of the variation in the wind-driven ocean circulation and the attendant changes in the development of forage organisms.

A study of the distribution and abundance of surface tunas (skipjack tuna and small yellowfin tuna) revealed that more schools are sighted near land than in the open ocean. In the open ocean more tuna schools were observed in the countercurrent than in the zone from the equator to lat 5°N, where deep-swimming yellowfin tuna are most abundant. Rather than respond to the general level of standing crop of forage, the surface tunas appear to respond to secondary factors that make it possible to forage more effectively. The distribution of "fronts" is such a secondary factor influencing the distribution of surface schools.

In 1949, before the establishment of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu,[3] the tuna resources of the equatorial central Pacific were little known and even less well understood. In the eastern tropical Pacific the Americans had a highly developed fishery for surface schools of yellowfin and skipjack tunas, and in the western Pacific the Japanese had an active longline fishery for the larger subsurface tunas. In the central Pacific, however, information on the tuna resources was limited to the experiences of a few commercial operators who had prospected in the area.[4]

From 1950 to 1953 the Bureau of Commercial Fisheries surveyed this unknown area, roughly the region between long 120°W and 180°, and between lat 15°N and 10°S. Studies undertaken during this period involved the distribution of tunas, the productivity of the waters, and the circulation of the ocean. The results of the surveys of the tunas form the substance of this report. Although the other investigations are detailed elsewhere, they are brought to bear wherever they help to explain the distribution of the tunas. Studies in the equatorial central Pacific

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[3] Then called the Pacific Oceanic Fishery Investigations. The facility is presently known as the National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory.

[4] It should be noted that today (1972) the oceanwide longline fishery is fully developed (see, for example, Suda and Schaefer, 1965). The results reported herein are representative of "virgin stock" conditions, and it is highly unlikely that a similar assessment can ever be repeated.

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after 1953 focused on special problems (Iversen and Yoshida, 1956) and are not considered in this report.

This paper on the equatorial tuna is in part documentary and summarizes the results of the Laboratory's experimental fishing and scouting; however, the major effort is a review of the distribution of yellowfin and skipjack tunas as it relates to the distribution of properties in the environment. To a lesser extent, we discuss two other tuna species, the albacore and the bigeye tuna. The results suggest that the abundance of yellowfin and skipjack tunas in the region varies according to the properties in the environment. The variation in abundance of deep-swimming yellowfin tuna in space and time is relatable to variations in the wind-driven ocean circulation that alter the rate of enrichment of the euphotic zone. How albacore and bigeye tuna are related to the environment is less clear. The occurrence of these species in deeper water than yellowfin tuna suggests that other factors may be of greater importance. The apparent abundance of surface tunas is not believed to be closely related to basic enrichment; rather, it appears that secondary factors, such as food-concentrating mechanisms, are more important.

Most of the data in this report have been published. The fish distributions have been described by Ikehara (1953), Murphy and Shomura (1953a, 1953b, 1955), Murphy and Ikehara (1955), and Shomura and Murphy (1955). The oceanographic data were published by Cromwell (1951, 1953), Austin (1954), Cromwell and Austin (1954), Cromwell, Montgomery, and Stroup (1954), Stroup (1954), and Stroup and Austin (1955). The plankton catches were reported by King and Demond (1953), Hida and King (1955), and King and Hida (1957).

SAMPLING METHODS AND MATERIAL

Longlining, trolling, and surface sighting, the latter supplemented by occasional live-bait fishing, were used to assess the abundance of tunas. None of these was completely satisfactory, chiefly because no single type of gear sampled all species and sizes of fish within each species with equal effectiveness. Further studies will undoubtedly reveal additional weaknesses in our general assumption that catches represent relative density of tunas.

Longlining

More effort was devoted to longlining (Figure 1) than to the other sampling methods, mainly because it proved to be the best way to capture significant numbers of tuna systematically.

Figure 2 shows the type of longline gear used during the survey. Niska (1953) gave details of its construction and operation. Basically the gear consists of (1) a mainline suspended at intervals from buoys and (2) branch lines that hang from the mainline, each with a baited hook. The amount of tackle between two buoys is called a "basket."

The mainline hangs slack in the water, presumably in the shape of a catenary (Figure 2). Since the mainline was 384 m long and the buoys were generally spaced about 274 m apart, the deepest hooks should have fished at about 152 m and the shallowest at about 76 m. The gear, however, fished at shallower depths than the expected depth because of differences in the forces exerted on the buoys by wind and surface currents and on the mainline by the deeper, sometimes opposing currents. Consequently the deep hooks may frequently have fished as shallow as 76 m (Murphy and Shomura, 1955).

At a typical longline station, 40 to 60 baskets of gear were set in the early morning and retrieved in the afternoon.

The longline catches are presented as numbers of fish per 100 hooks. Valid comparisons of availability can be based on this statistic, provided the construction of the gear and the operational details remain constant. Fortunately all of the catches were obtained in a nearly standardized manner that satisfied most of the assumptions, e.g., construction did not vary, roughly the same amount of gear was fished each day, and the fishing schedule was the same each day.

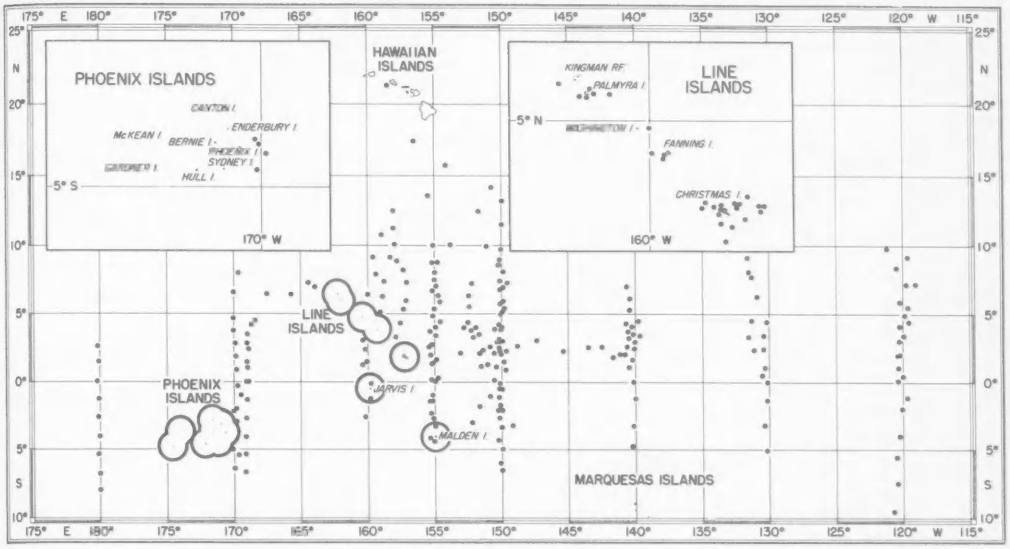

FIGURE 1.—Locations of longline stations. The circles show the location of an island or group of islands.

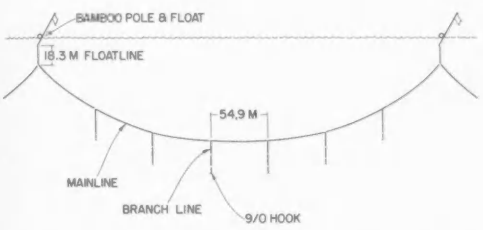

FIGURE 2.—Schematic diagram of tuna longline gear.

Trolling

Systematic trolling (Figure 3) provided another useful measure of tuna abundance. Generally when the vessels were underway (7-9 knots) two 45.7-m lines were trolled astern. A variety of tuna lures was used (Murphy and Ikehara, 1955). Occasionally near the islands, the "standard trolling" was modified by reducing vessel speed and trailing more than two lures. The catches from this type of fishing are considered separately from those of standard trolling.

Surface Sighting

As a further measure of tuna abundances, the abundance of surface schools of fish, bird flocks, and other signs of life was estimated by consistently maintaining a bridge log of sightings (Figure 3). A log of these observations was kept by the wheel watch under the supervision of the scientists on board (Murphy and Ikehara, 1955). These records provided a unique body of quantitative information on the bird and fish life in the central Pacific.

SPECIES OF FISH

Though the tunas are the most abundant and commercially most valuable of the large pelagic fishes in the central Pacific, a number of other species occupy prominent positions in the biota. The following list of species is largely based on longline catches, but it includes those likely to be captured by trolling or to be seen at the surface. The vernacular names listed below are used throughout the rest of this report.

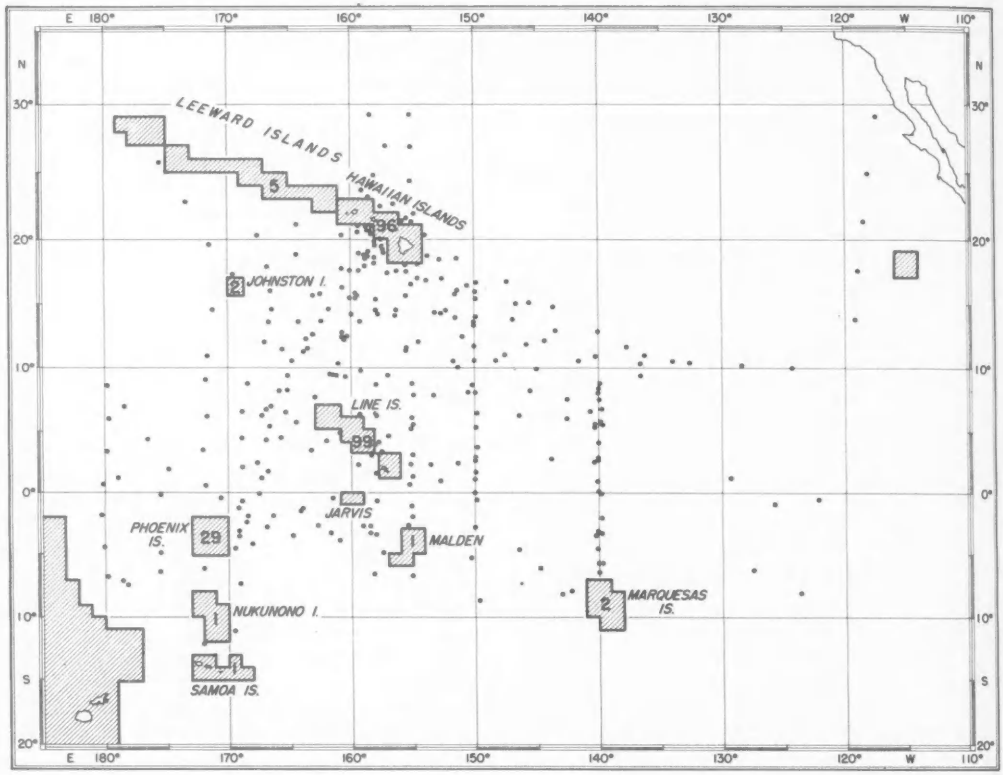

FIGURE 3.—Noon positions of vessels while trolling and surface sighting. Each dot represents the noon position for a day's observation. The number of days' observation in each of the shaded island areas (within 96.5 km of land) is shown by the figures. (Adapted from Murphy and Ikehara, 1955.)

Albacore, *Thunnus alalunga* (Bonnaterre)
Barracuda, *Sphyraena* sp.
Bigeye tuna, *Thunnus obesus* Lowe
Black marlin, *Makaira indica* (Cuvier)
Blue marlin, *Makaira nigricans* Lacépède
Blue shark, *Prionace glauca* (Linnaeus)
Dolphin, *Coryphaena hippurus* Linnaeus
Longnose lancetfish, *Alepisaurus ferox* Lowe
Mako shark, *Isurus* sp.
Oceanic whitetip shark, *Carcharhinus longimanus* (Poey)
Sailfish, *Istiophorus platypterus* (Shaw and Nodder)
Shortbill spearfish, *Tetrapturus angustirostris* Tanaka
Silky shark, *Carcharhinus falciformis* (Bibron)
Skipjack tuna, *Katsuwonus pelamis* (Linnaeus)
Striped marlin, *Tetrapturus audax* (Philippi)
Swordfish, *Xiphias gladius* Linnaeus
Wahoo, *Acanthocybium solanderi* (Cuvier)
Yellowfin tuna, *Thunnus albacares* (Bonnaterre)

ECOLOGICAL SUBDIVISION OF TUNAS

On the basis of size and behavior, populations of yellowfin tuna, bigeye tuna, and albacore can be conveniently separated into two groups: (1) the smaller surface fish and (2) the larger deep-swimmers. The two groups (Figure 4) cannot be readily sampled by any one fishing method; most surface fish are caught by trolling and live-bait fishing and most deep-swimmers by longline. This situation evokes a query as to whether the separation represents a real difference in vertical distribution or whether the two apparent groups result simply because one type of fishing is more effective for small fish and one for large. The differences in catch rates on longline hooks fished at different relative depths (Table 1) strongly suggests that large tunas do, in fact, tend to spend their lives well below the surface. For instance, the catches of large yellowfin tuna on the deep and intermediate hooks were half again as numerous as on the shallow hooks. The differences were even more striking for bigeye tuna and albacore.

The separation of the population into two components, surface and deep-swimming, is accompanied by a horizontal dichotomy, at least in the instance of yellowfin tuna. Sightings and troll catches of small yellowfin tunas (<36.3 kg) were usually associated with emergent land or shoals (Murphy and Ikehara, 1955). As will be discussed later in the section on surface tunas, the longline when fished in such insular areas captures significantly more small fish (as small as 2.3 kg) than when fished in the open sea (>96.5 km from land). When moving away from land, the reduction in numbers of small fish in the longline catch is proportional to the reduction in school sightings which suggests that small yellowfin tuna are associated with land.

There is another difference between deep-swimming and surface tuna. Generally, surface tuna gather in compact schools, which occasionally contain thousands of individuals, whereas Murphy and Elliott (1954) provided evidence from the serial distribution of yellowfin tuna catches along the longline that deep-swimming yellowfin tuna gather in small schools. Little in their data, however, suggests that these groups are anything more than loose aggregations of a few large individuals. Thus both the degree of aggregation and the principal depth range differ with size of fish, at least insofar as yellowfin tuna are concerned. For these reasons it is convenient, and probably realistic, to treat the two categories separately.

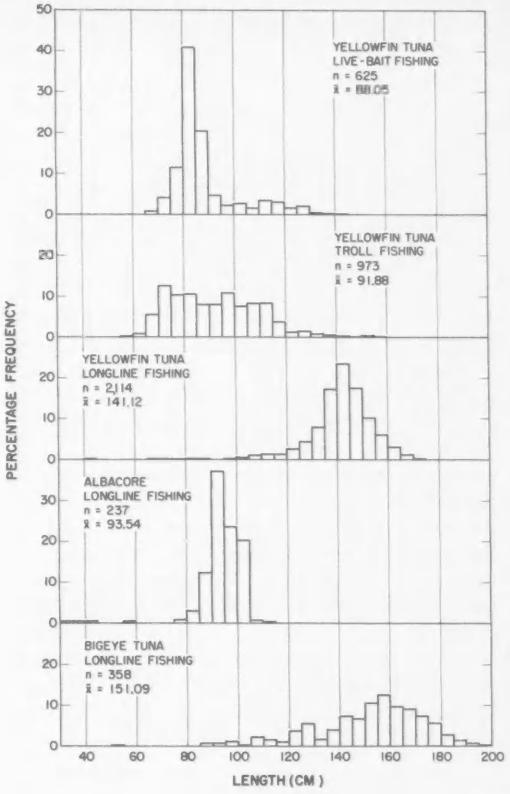

FIGURE 4.—Length frequencies (fork lengths) of the principal tuna species taken, by type of gear.

TABLE 1.—Yellowfin tuna, bigeye tuna, and albacore catches by relative hook depth (longline gear), 1950-53.

Tuna	Shallow	Intermediate	Deep	Total
Yellowfin	673	921	981	2,575
Bigeye	76	137	211	424
Albacore	10	68	122	200

DEEP-SWIMMING TUNAS

This section presents all the data on the distribution of deep-swimming tunas but emphasizes the yellowfin tuna and how the environment influences their distribution. Scientists have advanced certain hypotheses to explain the variations in the abundance of yellowfin tuna in the central Pacific (see, for example, Cromwell, 1953). These hypotheses, however, involve only portions of the total mass of data, and usually only a limited aspect of the variations in abundance, e.g., longitudinal variation.

The most elegant way to examine hypotheses about fish and the environment is to show step by step how precise interactions of energy flow and behavior (in a broad sense) result in a particular distribution of fish. This approach is not possible with the present data. Instead we have adopted the more generalized approach of advancing a hypothesis about one aspect of the data, i.e., the average distribution of yellowfin tuna with respect to the average distribution of environmental properties. Then we examine this hypothesis with respect to details of variation in abundance such as the north-south distribution and east-west distribution at particular times and places, and time variation at particular places. Our assumption is that if the same basic hypothesis stands up under this kind of cross-examination, its merit is essentially proved, even though a great deal remains to be learned about the exact way the ecosystem functions. This approach results in some repetition of arguments, especially as it has been possible to explain nearly all aspects of variation in abundance with the same hypothesis—namely, that variations in the dominant species, the yellowfin tuna, are influenced by variations in the wind-driven ocean circulation that affect the food supply of that species.

AVERAGE AREAL DISTRIBUTION

In this section we provide a brief description of the circulation of the major surface currents and the general distribution and relative abundance of the deep-swimming tunas and skipjack tuna in the central equatorial Pacific Ocean.

Oceanography

The dominant features of the eastern tropical Pacific are the three great currents (Figure 5): the westerly flowing North Equatorial Current

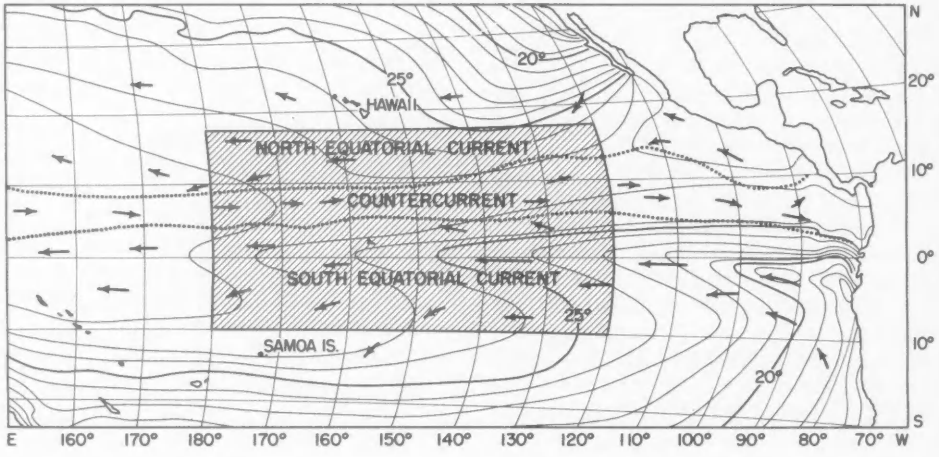

FIGURE 5.—Schematic representation of the major surface currents and surface isotherms in the central and eastern tropical Pacific. The area most intensively surveyed is shaded. Arrows denote approximate current direction. (Adapted from Schott, 1935.)

north of lat 10°N, the westerly flowing South Equatorial Current south of lat 5°N, and the easterly flowing equatorial Countercurrent lying between the two. Surface temperatures are generally high, mostly above 25°C.

Overlying the area are two major wind systems. The northeast trades blow over the North Equatorial Current and the southeast trades over the South Equatorial Current. Between them is a doldrum belt generally coinciding in latitude with the Countercurrent. The two equatorial currents are largely wind-driven, whereas the Countercurrent is simply the return flow caused by the piling up of the wind-driven water in the western portion of the Pacific. The speed of these currents at the surface is usually 1.85 to 3.70 km/hr (1-2 knots).

The configuration of the isotherms in Figure 5 shows that along any meridian the surface waters are cooler at the equator than in the adjacent waters to the north and south. This equatorial cooling is a result of wind-induced upwelling (Cromwell, 1953) and the divergence of water at the surface through the effect of the Coriolis Force. The Coriolis Force deflects the westerly moving water poleward, and this water is replaced by water rising from below (upwelling).

The equatorial upwelling, which brings deeper and enriched water upward into the euphotic zone, and the displacement of this water from the equator to a convergence south of the Countercurrent are the most important factors affecting the distribution of organisms in this region.

Tunas

The areal distribution of the large deep-swimming tunas can best be visualized from contour maps (Figures 6, 7, and 8). This series of diagrams was prepared from the catches of the Laboratory's longline fishing cruises (Figure 1) and the catches of several Japanese vessels (Murphy and Shomura, 1955; Shomura and Murphy, 1955). The presentation suppresses the random and temporal variability, yet it does convey the major features of the tuna distributions. It should be noted that the units used in contouring were those suggested by the catches.

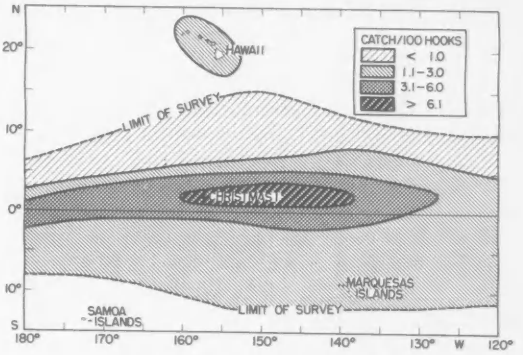

FIGURE 6.—The distribution of deep-swimming yellowfin tuna in the equatorial central Pacific. The isograms are in units of number of fish caught per 100 hooks.

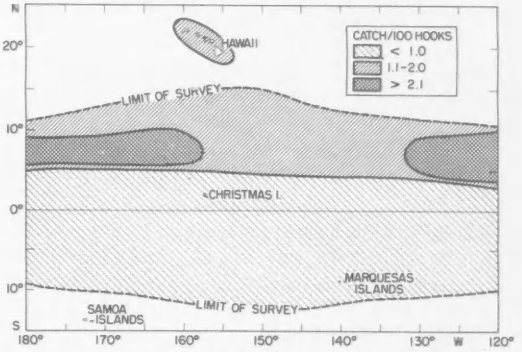

FIGURE 7.—The distribution of deep-swimming bigeye tuna in the equatorial central Pacific. The isograms are in units of number of fish caught per 100 hooks.

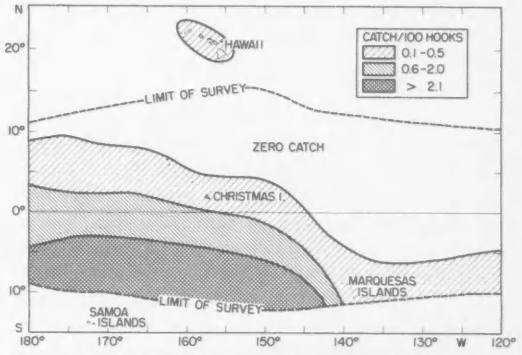

FIGURE 8.—The distribution of deep-swimming albacore in the equatorial central Pacific. The isograms are in units of number of fish caught per 100 hooks.

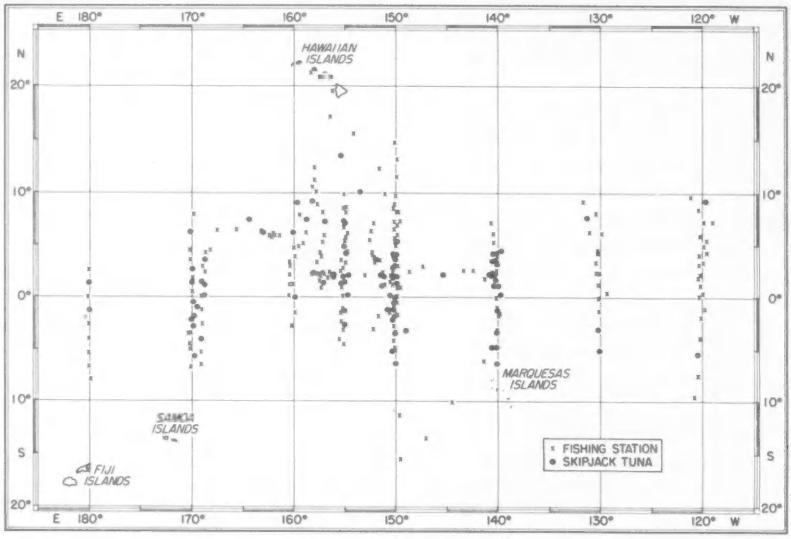

FIGURE 9.—The distribution of skipjack tuna in the equatorial central Pacific Ocean as shown by longline catches. A dot represents capture of one or more skipjack tuna.

Yellowfin tuna were found over the entire survey area (Figure 6), but the peak abundance occurred near the equator in the zone enriched by the equatorial upwelling. Between this zone and lat 10°N, the numbers decreased rapidly. Abundance south of the equator also declined but not as precipitously as to the north. Even near the equator this species was scarce at the eastern end of the survey area; it was most abundant in the center (between long 140° and 160°W) and somewhat less abundant to the west of long 160°W.

Bigeye tuna were not as abundant as yellowfin tuna, but their distribution, like that of the yellowfin tuna, was far more uniform over the area covered (Figure 7). On the basis of the small catches, two tongues of relatively high abundance were at the two ends of the survey area (Figure 7). These tongues, lying between lat 5° and 10°N, roughly coincide with the zone of the Countercurrent.

The distribution of albacore resembled neither that of the yellowfin nor the bigeye tunas. They were most numerous in the southwestern portion of the survey area (Figure 8) and their abundance declined to the northeast. Additionally, a broad zone to the north appeared to be completely devoid of the species. The reasons for this distribution are not at all clear.

In addition to the yellowfin tuna, bigeye tuna, and albacore that fit our definition of deep-swimming tunas, the longline captured a few skipjack tuna (Figure 9). The skipjack tuna is a smaller species (rarely over 18 kg) than the longline is designed to capture. Nevertheless, the gear is not absolutely selective because it has taken skipjack tuna as small as 2 kg.

The sporadic catches of skipjack tuna by longline are too scanty to estimate relative abundance and are therefore indicated in Figure 9 only as locality records. The skipjack tuna were present over a vast area of the central Pacific. Studies of the distribution of tuna larvae (Matsumoto, 1958) suggest that skipjack tuna are more abundant than yellowfin tuna in the central Pacific, the implication being that the equatorial central Pacific has a large underutilized stock of skipjack tuna.

SIZE OF DEEP-SWIMMING YELLOWFIN AND BIGEYE TUNAS

Though several species of tuna were taken by longline in the central Pacific, only the samples of yellowfin and bigeye tuna were substantial enough to warrant analysis of length differences by area. Iversen (1955, 1956) indicated that there were no significant changes in the size of yellowfin and bigeye tunas that could be related to time. Because of the wide temporal and spatial gaps in sampling, we confine ourselves to a descriptive summary of size differences with area. Most of the samples were taken between lat 5°N and 5°S and, as might be expected, no pronounced size differences were associated with latitude (only stations 96.5 km or more from land were considered in this analysis); only size differences associated with longitude are left for consideration.

To describe length differences more fully, we include data from the western Pacific (Murphy and Otsu, 1954) as material from the primary study area. We pointed out in an earlier paper (Murphy and Shomura, 1955) that the lengths of deep-swimming yellowfin and bigeye tunas differ across the equatorial Pacific. Since essentially the same gear has been used to sample the tuna in all areas, these changes must reflect some biological attributes of the populations.

Length frequencies for several longitudes shown in Figure 10 suggest a trend to smaller yellowfin tuna in the western Pacific. The essentials of the material in Figure 10, more succinctly shown in Figure 11, suggest a rather regular cline along the equator with respect to

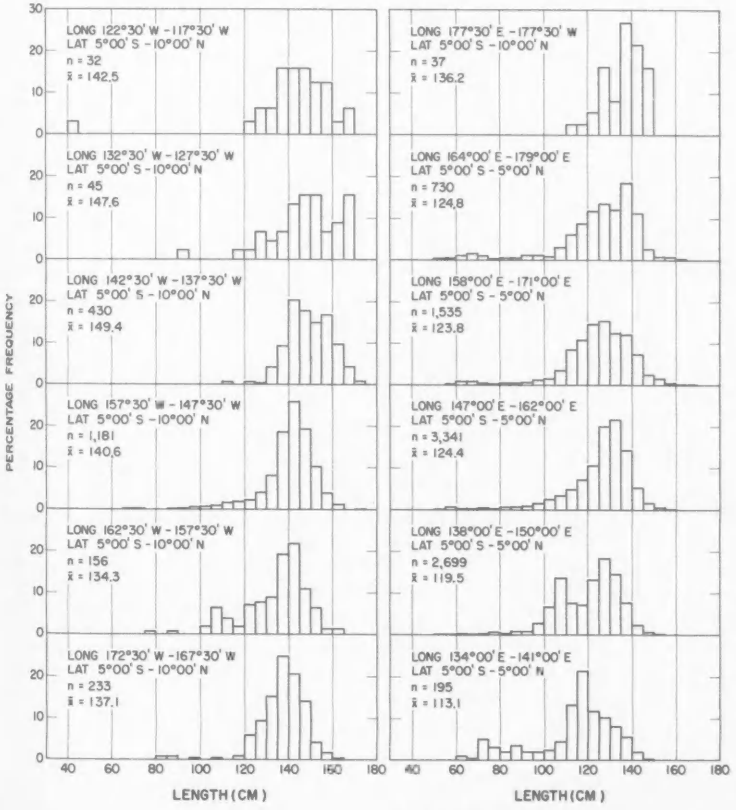

FIGURE 10.—Length frequencies of longline-caught yellowfin tuna by longitude of capture between lat 10°N and 5°S.

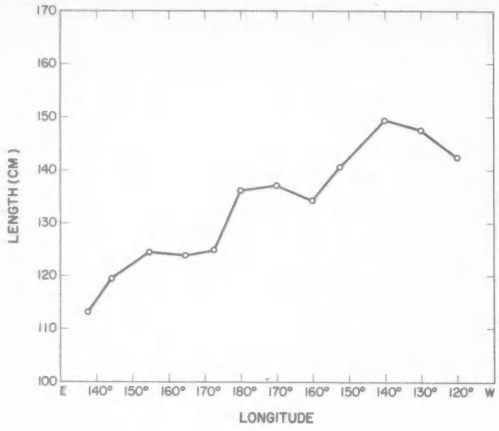

FIGURE 11.—Mean lengths of longline-caught yellowfin tuna.

average length. This same phenomenon is also evident for the bigeye tuna (Figures 12 and 13), which lends greater credibility to the view that the cline is not an artifact of the sampling system but due to a biological process.

This shift in length is reflected in other attributes of the populations. As indicated in Figure 14, males outnumbered females among the larger yellowfin tuna. Furthermore, the length at which males clearly dominate increases from west to east, as the average size of the fish sampled increases. Males also dominate the larger sizes of bigeye tuna (Otsu, 1954; Shomura and Murphy, 1955) but our data for this species are not adequate to examine the possibility that the length at which males dominate changes from west to east.

In addition to these clines, Royce (1953, 1964), in a study of yellowfin tuna morphometrics, dem-

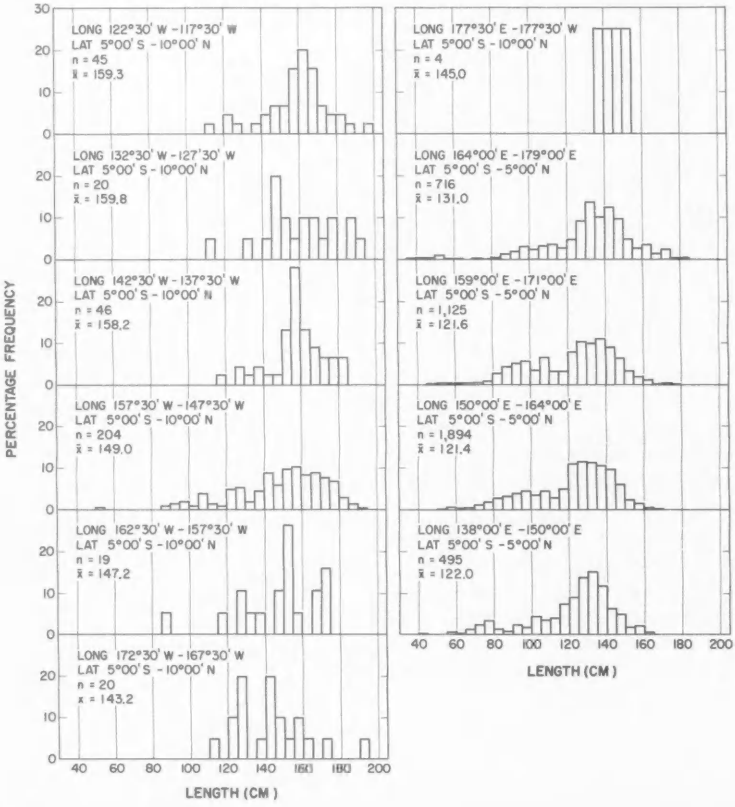

FIGURE 12.—Length frequencies of longline-caught bigeye tuna, by longitude of capture, between lat 10°N and 5°S.

onstrated east-west clines in the body proportions of yellowfin tuna taken in equatorial waters. For example, fin lengths decreased and head lengths increased to the east. Thus, along the equator we find more or less uniform clines in the yellowfin tuna of such biological characters as size, size at appearance of sex-ratio variations, and morphological characters. Limited evidence also suggests that the same phenomena are present in the bigeye tuna.

Inquiry into the basic causes for the east-west clines is somewhat speculative at the present time. Royce (1953, 1964) considered the morphometric evidence and concluded that the equatorial yellowfin tuna are made up of semi-independent stocks. Iversen (1956) focused his attention primarily on east-west size differences and suggested that the differences are maintained by easterly migration as the fish grow larger. An additional factor entering Iversen's hypothesis is that the number of small yellowfin tuna around the Line Islands, the only islands in the immediate vicinity of the equatorial central yellowfin tuna population, does not appear to be large enough to account for the sizable numbers of large deep-swimming yellowfin tuna in this general area, inferentially suggesting that recruitment must involve migration from somewhere else—the west, according to Iversen.

Conceivably recruitment could occur by movement of yellowfin tuna in a north-south direction, for there are large numbers of small islands in French Oceania, some 1,112 km (600 miles) to the south of the equatorial area. Small yellowfin tuna are known to occur near the surface around those islands (Royce, 1954), and the populations there, if extensive, could supply the necessary recruits to the large population of deep-swimming yellowfin tuna. This postulated movement, however, would be contrary to the conclusion reached by Royce (1964, p. 427) that "... most yellowfin tuna probably remain within a few hundred miles of where they occur as post larvae."

The length gradient of deep-swimming fish, with the attendant dearth of large fish in the west and small fish in the east, remains a strong argument favoring extensive west-east migration. If it is argued that there is no migration

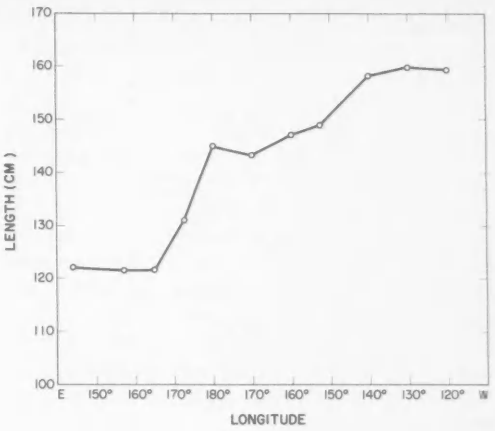

FIGURE 13.—Mean lengths of longline-caught bigeye tuna.

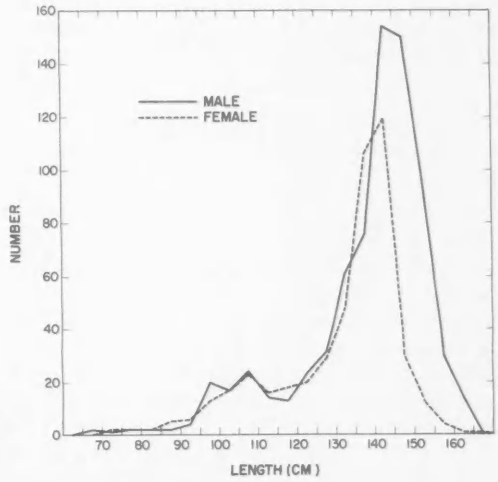

FIGURE 14.—Length distribution by sex of longline-caught yellowfin tuna (data from catches made in 1953).

and that the gradient exists simply because yellowfin tuna grow more slowly in the west, where the basic productivity is lower (Murphy and Otsu, 1954), there remains to be explained the relative scarcity of medium-sized fish in the eastern catches of deep-swimming tunas. This difficulty could be overcome by proposing that the

adoption of the deep-swimming habit is age-specific rather than size-specific and that the smaller fish are scarce in eastern longline catches because they are not old enough to adopt the deep-swimming habit. This proposal is not as farfetched as it might seem, for albacore appear to adopt the deep-swimming habit at a size (about 13.6 kg) at which yellowfin tuna still school at the surface. Furthermore, the fact that the size at which males dominate the catches increases, as the average size of the individuals in the deep-swimming population increases (Figure 14) argues against migration and suggests that at least some physiological changes are age-specific. Behavior changes might easily be among these age-specific attributes.

In summary, there are east-west clines in morphological and other biological characters of the catches. These clines can be explained by migration, if one chooses to ignore the evidence of morphometry and the changes of size at the onset of male dominance. If the clines are attributed to genotypic or phenotypic changes in relatively sedentary stocks, all available evidence can be accepted, but additional assumptions such as slower growth rate in the west and age-specific behavior changes must be introduced.

MERIDIONAL DISTRIBUTION

In a preceding section we examined the ocean and the fish populations in plane view and concentrated on the descriptive aspects. Most of the prominent features of the environment and the fish populations are zonally aligned, and the relations among the several fields can be most effectively visualized when their properties are examined in a meridional section. In presenting the details of the oceanography, the tuna distribution, and the tuna-oceanography interrelation-

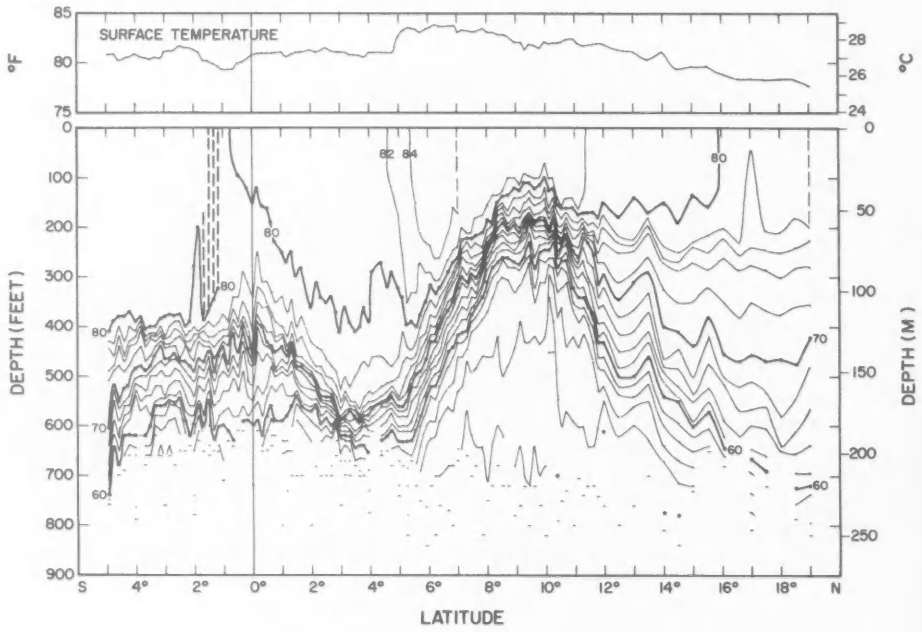

FIGURE 15.—Meridional temperature section based on bathythermograms, *Hugh M. Smith* cruise 11 along long 150°W (Austin, 1954b).

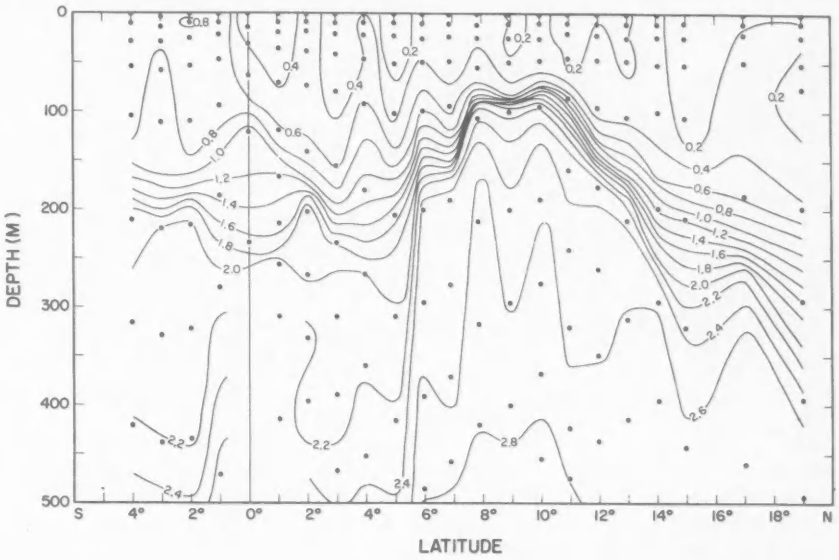

FIGURE 16.—Distribution of inorganic phosphate along long 150°W, September 26 through October 4, 1951, *Hugh M. Smith* cruise 11. PO_4 in micrograms per liter, isopleth intervals 0.2 μg atom per liter (Austin, 1954b).

ship, we have elected to use long 150°W, because more information is available from that meridian than from any other and it lies in the center of the region in which yellowfin tuna are most abundant (Figure 6).

Oceanography

A meridional temperature section along long 150°W (Figure 15) clearly shows the several features described in plane view (Figure 5). North of lat 10°N the isotherms sloping to the right indicate the westerly flowing North Equatorial Current. Between lat 10° and 5°N the isotherms slope to the left, indicating the easterly Countercurrent. South of the Countercurrent lies the westerly flowing South Equatorial Current.

The cool water at the equator is the result of divergence which disturbs the stability of the thermocline and thereby increases the rate of upward diffusion (upwelling). Under these conditions the surface waters are always cooler than adjacent waters. Nutrient salts, such as phosphate (Figure 16), are also affected, and their distribution suggests that nutrients are diffusing into the euphotic zone near the equator faster than they are being utilized. According to Cromwell (1953), these enriched waters moving northward and southward within the framework of the westerly flow are warmed and the nutrients are utilized by organisms.

Between the upwelling at and near the equator and the southern boundary of the Countercurrent at about lat 5°N (Figure 15), there is convergence and sinking of the northward flowing waters (Cromwell, 1953). The downward sloping arrows in Figure 17 show schematically the convergence with its attendant sinking. Among other features shown in the figure are the easterly flowing Countercurrent (flow is toward the observer), the westerly North Equatorial Current to the north, and the westerly South Equatorial Current to the south. The figure also

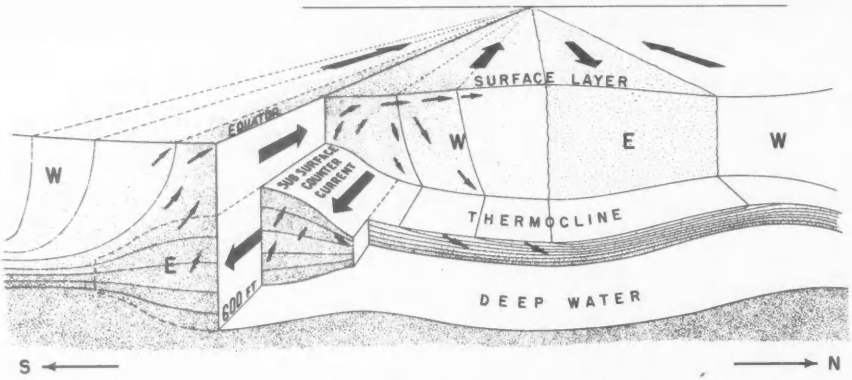

FIGURE 17.—Schematic representation of a meridional section of the equatorial central Pacific (Sette and staff of P.O.F.I., 1954, p. 3).

shows a feature new to this discussion, the Equatorial Undercurrent described by Cromwell, Montgomery, and Stroup (1954). This latter current is usually found in the upper portion of the thermocline and rarely flows as a surface current.

Tunas

Our aim is to compare the meridional distribution of fish with certain properties in the environment. Ideally, we should compare the weight of fish life at a given trophic level with such elements as plankton abundance and nutrient level. This comparison is difficult with the material at hand, but, as shown in Appendix A, the catches of yellowfin tuna, the dominant species, appear to reflect the abundance of the larger predators.

Tuna-Oceanography

In the discussion of the areal distribution of tunas we pointed out that the peak abundance of yellowfin tuna was near the equator. We now propose to examine the hypothesis that this striking concentration of yellowfin tuna is the result of the following sequence of events: (1) upwelling at the equator, (2) northward displacement of the water, (3) relatively rapid development of zooplankton, (4) a slower development of tuna forage, and (5) congregation of tuna in the region best supplied with forage.

It can be inferred from the distribution of yellowfin tuna and water temperature in Figures 6 and 15 that there is a general coincidence between the location of upwelling and the zone in which yellowfin tuna are most abundant. Figure 18 clearly shows this relation as well as the distribution of other variables such as plankton and current direction.

In the top panel (A), the temperature structure shows the cool surface waters at the equator that can be attributed to upwelling. That this is accompanied by enrichment was shown in Figure 16 in the distribution of inorganic phosphate. The sharp downward slope of the isotherms between lat 5° and 9°N is the region of the Countercurrent.

The second panel (B) shows the drift of the longline while in the water. This drift, which is essentially the movement of the gear between 0600 and 1600 hr, shows the direction of the several major water movements discussed earlier. North of lat 9°N, the drift is to the west, indicating the North Equatorial Current. Between lat 5° and 9°N, the drift is to the east, suggesting the Countercurrent. Except for the station nearest the equator, the drift is westerly south of lat 5°N, indicating the South Equatorial Current. The easterly drift at the equator is

probably caused by the easterly flowing Equatorial Undercurrent (Figure 17). It should also be noted that each side of the equator has a poleward component to the longline drift. These observations confirm empirically the conclusion by Cromwell (1953), based on theoretical considerations, that divergence at the equator leads to upwelling and that this enriched water moves poleward.

In the third panel (C), zooplankton is shown to be most abundant at the center of upwelling, falling off more precipitously to the north than to the south. The zooplankton reaches a maximum at or near the equator, where the upwelling is centered (panel A). The model proposed by Cromwell (1953) requires a net transport of water away from the equator, and because the zooplankton sampled is at least one trophic level removed from chemical nutrients, we might expect its peak abundance to be significantly displaced from the site of upwelling. The magnitude of the displacement would be a function of the rapidity with which the zooplankton reaches a peak, the speed of the north-south transport, and possibly the rate of grazing.

Since no displacement was observed in a series of stations spaced at 96.5-km intervals, the possible conditions include: (1) the zooplankton develops very rapidly, (2) the north-south transport is slow, (3) grazing is highest just north and south of the equator, or (4) a combination of the three factors. Nothing is known of the development rate of equatorial zooplankton (chiefly copepods), but some marine cladocerans have been reported (Wickstead, 1963) to reach a peak in 36 to 40 days at temperatures higher than 28°C. Assuming this rate of development for the equatorial zooplankton, a poleward displacement of water as rapid as 6.4 km a day would be readily detected in plankton hauls spaced 96.5 km apart. The lack of a displacement suggests that grazing may be an important factor controlling the spatial distribution of the standing stock of zooplankton in equatorial waters.

In addition to the lack of horizontal displacement of the peak of zooplankton from the equator (Figure 18), the plankton volumes south of the equator were slightly larger than those to the

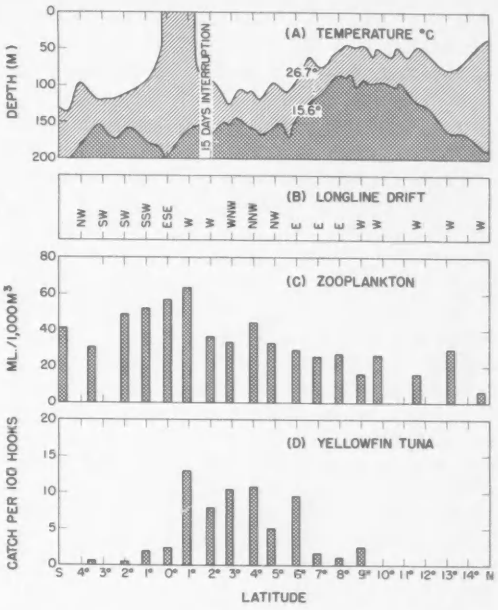

FIGURE 18.—Diagrams of several fields resulting from a section along long 150°W in September 1951. A. Temperature section from bathythermograms. B. Direction of longline drift at each fishing station. C. Volumes of zooplankton at each fishing station. D. Catch rate of yellowfin tuna at each fishing station. (Adapted from Sette, 1955.)

north. This situation, however, is not the usual one because King and Hida (1957) reported that the average standing crop of plankton is greater between lat 1.5°N and the southern boundary of the Countercurrent (about lat 5°N) than between lat 1.5° and 5°S. This general situation is thought to be the result of the dominance in this region of the central Pacific southeast trades which, according to Cromwell (1953), transport most of the enriched water northward. In the present instance, the longline drifts (Figure 18, panel B) give evidence that the momentary major transport was to the south of the equator. Thus, the observed asymmetry of the plankton is consistent with the momentary circulation.

The yellowfin tuna catches (Figure 18, panel D) show even less symmetry about the equator

than the plankton. This asymmetry seems anomalous until it is considered in the light of the general northward transport of the enriched water and the probable time required for tuna forage to appear after the enrichment at the equator.

Tunas do not consume the smaller zooplankters that make up the bulk of the catches of the 1-m nets of 30×××gage mesh used to sample zooplankton. Rather, tunas forage on the higher trophic levels, from euphausiids to all but the largest nekton (Reintjes and King, 1953). If the food supply is the chief determinant of tuna abundance, the tunas, which are capable of rapid and extensive migration, will concentrate where they can most readily obtain food. In the absence of poleward motion we would presume that tuna forage as well as tunas would concentrate or develop at the equator, where the enrichment and the zooplankton are centered. There is poleward motion, however, and the successive trophic levels above the zooplankton would be expected to have their greatest population density at some distance from the equator.

SPACE AND TIME VARIATION

In this section we focus attention on the variation in the distribution of yellowfin tuna and the variation in distribution of properties in the environment and attempt to show their relation. The zone between the equator and the Countercurrent receives primary attention simply because more information is on hand from this area than from others.

Space and time variation in the tuna distribution have been discussed in earlier publications. Murphy and Shomura (1953b) pointed out that when and where southeast winds prevailed the yellowfin tuna seemed to be concentrated north of the equator; when northeast winds prevailed the yellowfin tuna were concentrated south of the equator; and during periods of variable winds they straddled the equator. These observations were amplified and further discussed by Sette (1955, 1958), who suggested that the average distribution of the catch rates might well be a function of geographical variation in the strength of the trades, if a suitable but unknown lag period is assumed between maxima of upwelling and the occurrence of tuna forage.

The waters of the equatorial current system are in a state of constant flux, with upwelling, poleward motion, sinking, and westerly motion integrated into a whole that represents a continuously changing environment. In this environment we have made "instantaneous" observations at selected points and times, and as expected the data obtained are dissimilar in respect to space and time. In theory, at least, a true concept of the relative magnitudes of the several components of the water motion should make it possible to unify these results into a coherent whole. It appears that vertical motions (upwelling) and sinking (convergence) are counterbalancing within the geographical limits (north-south) of the area under consideration, but the relative strengths of the westward and northward motions, which cannot be counterbalancing, have not been adequately defined.

Sette (1958), in interpreting the then available information, assumed that the western component of flow near the equator was of overriding importance in comparison with the poleward flow associated with divergence and upwelling. This assumption is consistent with the mean surface flows indicated in climatological-type summaries of ship's drift observations (e.g., Figure 5) but is not consistent with certain empirical determinations derived from the drifts of longlines and drogues. These determinations suggest that the average poleward component of motion to the north of the equator on long 120°W would bear little relation to events at lat 5°N on long 140°W and even less to events at lat 5°N on long 150°W. In other words, water parcels upwelled at the equator on long 120°W are probably lost from the system by the time they are transported westward to long 130°W, because their northward motion will have carried them to the Countercurrent (near lat 5°N). Here, they must sink because the Countercurrent is warmer and less saline than the waters to the south.

Most of the evidence for these arguments lies in measurements of the drifts of sets of longline

gear. The longline, which is suspended from the surface to the thermocline, gives a useful measure of the net movement of the mixed layer. Between the surface and the thermocline are about 512 linear meters of 0.635-cm diameter cotton line having about 10.2 sq m of surface for each basket of gear. The buoys that support the line are acted on by the wind, but they present only about 0.56 sq m of surface to each basket of gear. Typical sets consist of 40 to 60 such units, which are in the water about 10 hr. Since the gear is set at dawn, the morning fixes based on celestial navigation provide a good starting point. Because the last unit (first one set) is retrieved at about 1600 hr, it is necessary to rely on sun lines, dead reckoning, and the evening stars for the final position determination.

This procedure is routine during longline fishing surveys, but most determinations of drifts of the gear are somewhat unreliable for various reasons. There are, however, 14 measurements from the area between long 140° and 155°W and between the equator and lat 5°N that appear reliable within the limits of celestial navigation. These given a mean northward motion of 0.67 km/hr (0.36 knot) and a mean westward motion of 1.06 km/hr (0.57 knot), or a ratio of 1 to 1.6. Wind effect on the longline sets is unknown, but the relative amount of exposure to the two forces and the relative viscosities of the water and air suggest it is negligible. It can also be argued that the sample of 14 measurements is inadequate, and this cannot be denied. The 14 measurements were, however, well scattered in time and space and vary so markedly from pilot-chart summaries that we feel a revision of the existing concept is in order.

In addition to the longline drifts, special measurements of the motion of the surface water north of the equator were made in August 1952 by using drogues (Cromwell, Montgomery, and Stroup, 1954). A surface drogue placed in the water at lat 0°01'N, long 149°31.5'W, moved to lat 2°48.5'N, long 151°42'W in 10 days. The mean westward component was 0.85 km/hr (0.46 knot) and the northward component 1.18 km/hr (0.64 knot), values that are relatively consistent with the longline drifts.

Such high rates of northward flow seem to imply an exceedingly rapid rate of upwelling, which should possibly be characterized by an even more marked cooling at the equator than is indicated by the measurements at hand. In this regard, however, several factors must be considered. Although we do not know the depth from which water is being upwelled, it is most likely to be coming from near the top of the thermocline, where the temperatures are not strikingly low (Figure 15). A further complication is the possible return flow along the top of the thermocline towards the equator suggested by Fofonoff and Montgomery (1955). This mechanism could return water that has converged north of the equator to the undercurrent, where it might be enriched and re-upwelled. Thus, even rapid north-south circulation and upwelling at the equator do not necessarily call for intense cooling at the equator.

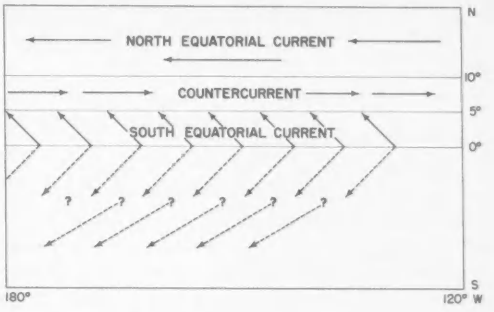

FIGURE 19.—Schematic view of the equatorial current system incorporating recent empirical determinations of flow north of the equator. Flow south of the equator is indicated as questionable.

These arguments show that the circulation between the equator and the Countercurrent is exceedingly complex and as yet imperfectly known. There is, however, enough evidence to suggest that the region between long 120°W and 180° is not a single east-west system with respect to identity or homogeneity of origin of its water. The available evidence indicates that it should be regarded as a series of adjacent homologous northwesterly flowing circulation cells (Figure 19). As will be demonstrated, the distribution of properties, e.g., nutrients, plankton, and fish,

is more readily reconcilable with this concept than with the classical flow pattern depicted in Figure 5.

Geographical Variation

We have advanced the concept that the flow pattern in the northern latitudes of the equatorial waters consists of a series of homologous northwesterly flowing cells. A study of the distribution of physical and biological properties, e.g., winds, water temperature, nutrients, plankton, and fish, indicates that they are more readily reconcilable with the homologous cell concept than with the classical flow pattern depicted in Figure 5.

Winds.—The wind system is the source of energy for the equatorial circulation, and it is logical to approach the problem of geographical variation of tuna by first examining the variations in the winds. The average distribution of winds (Figure 20) clearly shows a peak of wind stress near long 130°W, and in this area the equator is dominated by the southeast trades. Farther west the two trade systems are about equally distributed and the average force declines. In the far west the northeast trades dominate and the average force is low.

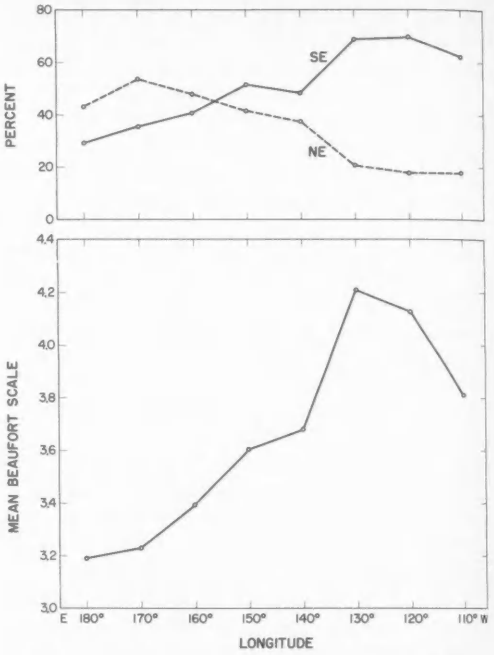

FIGURE 20.—Average direction and force of winds over the equator. The values were derived from U.S. pilot charts for 1953. In arriving at a value for a given longitude we averaged the winds in the four 5° squares focusing on the intersection of the meridian and the equator. East winds were apportioned equally between northeast and southeast.

Water temperature.—If the wind is the causal force behind the upwelling and poleward displacement of enriched (cooled) water, there should be a demonstrable relation between variation in the mean wind and variation in the mean water temperature. Table 2 depicts the mean monthly temperature of the surface waters north of the equator. It clearly shows the general trend to warmer water in the west in the zone between the equator and lat 5°N, which is the expected result of the wind gradient (Figure 21).

More significant is the variation in the size of the water temperature gradient from east to west. For instance, during March there is practically no slope but during October there is a steep slope (Table 2). The size of these gradients, when plotted against a measure of the gradient of southeasterly winds (Figure 21), suggests a causal relationship. When the wind gradient is large the gradient in water temperature is steep, and vice versa. We can now proceed with confidence on the assumption that variations in the winds are responsible for variations in water temperature through altering the rates of upwelling and the northward displacement of cool water.

Nutrients.—It is now in order to examine the distribution of nutrient salts in the euphotic zone along the equator to see whether the concentration varies with the amount of upwelling as evidenced by winds and water temperature.

TABLE 2.—Mean surface temperatures by longitudes and months for lat 0° to 5°N (basic data from U.S. Weather Bureau, 1938).

Month	Longitude west						
	110°	120°	130°	140°	150°	160°	170°
January	24.9	25.7	25.0	25.7	26.3	26.7	27.2
February	25.6	25.6	25.7	26.2	26.1	26.2	27.0
March	26.6	26.2	25.9	26.7	26.8	26.7	26.7
April	26.8	27.1	26.4	26.6	26.9	26.9	27.2
May	27.1	26.9	26.4	26.8	27.1	27.1	28.0
June	26.1	25.9	26.8	27.7	27.6	27.5	27.9
July	25.1	25.6	25.9	26.6	26.9	27.3	27.5
August	24.6	25.1	25.6	26.0	26.7	27.1	27.7
September	24.6	24.6	24.9	26.0	26.7	27.2	27.8
October	24.4	24.6	25.3	25.9	26.9	27.3	27.7
November	24.9	25.1	24.9	26.0	26.7	27.3	27.3
December	24.9	25.1	25.1	25.2	26.1	26.4	27.3
Mean	25.4	25.6	25.7	26.3	26.7	27.0	27.4

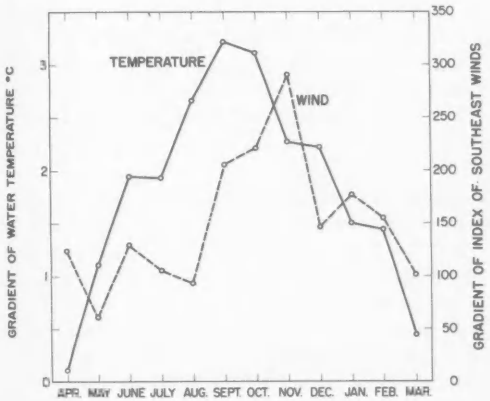

FIGURE 21.—Gradients of mean surface water temperature, equator to lat 5°N, and stress of southeast winds across the equator between long 120° and 170°W. We prepared the index of southeast wind stress by multiplying the percentage occurrence by the average force. The basic data are from the four wind roses that focus on the intersection of the equator and the appropriate longitude in the U.S. pilot charts for 1953. Half of the due east winds were arbitrarily assigned to the southeast quadrant.

Because of the lack of measurements of other salts, we will consider only inorganic phosphate. Even a discussion limited to this property must be considered poorly documented, however, because of the few measurements and the inherently erratic nature of phosphate determinations.

In considering the distribution of phosphate, we have constructed several temperature-phosphate curves from along the equator (Figure 22). We elected to use the temperature-phosphate curve because it seemed to yield the best available index of enrichment. Although low temperatures appear to be a good index of upwelling and relative enrichment when a single meridional section is being considered, it does not necessarily follow that relative coolness among meridians along the equator is a good index of enrichment, for there are marked east-west gradients in such factors as the depth of the thermocline (Austin, 1958). Temperature-phosphate curves should permit evaluation of the differences associated with these gradients and should indicate the "enrichment potential" along the equator.

The surface temperature relations among the temperature-phosphate curves in Figure 22 are consistent with the general east-west distribution of temperature, i.e., cooler water to the east suggests that they represent typical rather than atypical conditions. Phosphate, however, does not follow temperature when the several longitudes are considered together. Inorganic phosphate is lowest along long 117°W, where the surface water is coldest, and highest along long 140°W, where water temperature is intermediate. These differences in the basic temperature-phosphate relation appear to persist to rather low temperatures and therefore to considerable depths.

We will not attempt to explain the differences

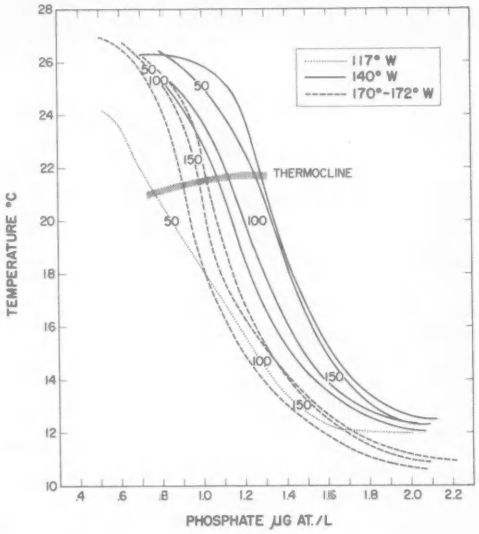

FIGURE 22.—Temperature-phosphate curves from the equator at several longitudes. The thermocline approximately corresponds with the 21°C isotherm. The approximate depth in meters for each group of curves is shown. Where one longitude is represented by several curves, the stations are separated in time from several weeks to several months.

in the distribution of phosphate. Accepting the differences among longitudes (Figure 22) as valid, it is clear that, though inequality in wind stress might be directly related to the amount of upwelling and consequently of cooling of the euphotic zone (as appears to be the case), these inequalities in wind stress will not necessarily be directly related to variations in the amount of enrichment. A given wind stress will probably produce the most enrichment along long 140°W, whether the energy is chiefly dissipated in the region of the thermocline or is dissipated uniformly with depth. The difference, however, will be most striking if the principal effect of the wind is expended in disturbing the thermocline. For instance, water diffused up from the thermocline along long 140°W will contain nearly twice the amount of nutrient salts as water diffused up from the thermocline at long 117°W.

Considering the variations in the vertical distribution of nutrient salts (Figure 22) and the geographical distribution of wind stress (Figure 20), it appears that on the average the greatest enrichment might be in the center of the system (near long 140°W), for in this region wind stress is high and the thermocline is abundantly supplied with nutrients. To the west, enrichment could very well fall off, since the wind stress declines, and to the east, enrichment might decrease because the thermocline is impoverished.

The discussion above is admittedly based on scanty and perhaps unreliable data. The general conclusion—that we should expect the most enrichment near the center of the area under consideration—is, however, compatible with the biological data to be considered next. Even more important, the phosphate-temperature curves indicate an east-west heterogeneity in the distribution of physical and chemical properties. This heterogeneity is consistent with the model of flow pattern (Figure 19) evolved from longline drift data.

Biological properties.—The biological properties along a latitudinal axis (Figure 23B, C) do not follow the temperature gradient (Figure 23A and Table 2) but rather tend to be distributed in conformance with the general enrichment pattern described in the previous section on nutrients. Both plankton and yellowfin tuna tend to be highest in the center of the region, where the measurements suggest enrichment is greatest.

The plankton distribution (Figure 23B) is somewhat unreliable to the east of long 150°W because the samples are few and unequally distributed in time (King, 1954; King and Hida, 1957). Nevertheless, all evidence points to a peak of plankton coinciding with or slightly west of the peak in enrichment.

The distribution of yellowfin tuna (Figure 23C) is more orderly than that of zooplankton, possibly because of a more orderly temporal and spatial stratification of the samples. The peak abundance of tuna is close to the longitude of maximum enrichment and the longitude of maximum standing crop of zooplankton.

Though there is general agreement between the standing crop of zooplankton and tuna, there are several discrepancies. For instance, the

high in zooplankton volume is only about 50% greater than the low, whereas for yellowfin tuna this difference is about 300%. These facts could indicate the inadequacy of some of the implicit assumptions, such as the standing crop of zooplankton is a measure of the standing crop of tuna forage, and the latter is a measure of the abundance of tuna; the longline catches are a measure of the abundance of yellowfin tuna; the abundance of yellowfin tuna is representative of its trophic level; and the system is equally efficient at all levels. Nevertheless, the general correspondence of the peak of zooplankton and yellowfin tuna appears more than casual (King and Hida, 1957).

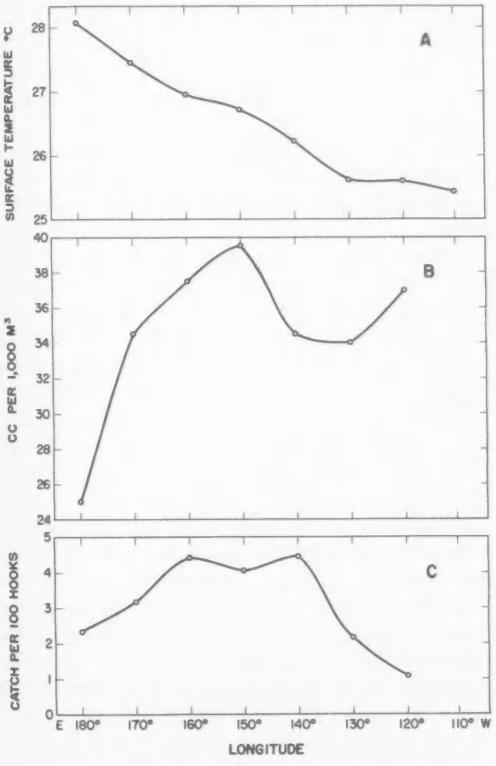

FIGURE 23.—A. Mean surface temperature from the equator to lat 5°N (U.S. Weather Bureau, 1938). B. Mean zooplankton from lat 5°N to lat 5°S (King and Hida, 1957). C. Mean yellowfin tuna catch from lat 5°N to lat 5°S.

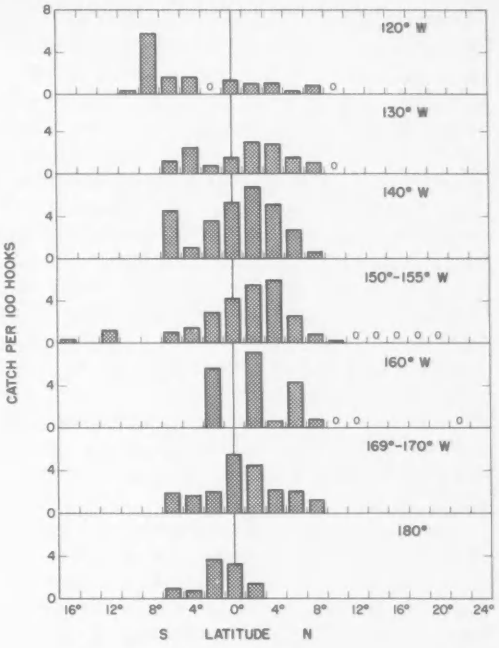

FIGURE 24.—Mean distribution of deep-swimming tuna. (The zero figures in the panels represent fishing effort expended, but no catches made; all stations 96.5 km or more miles from land.)

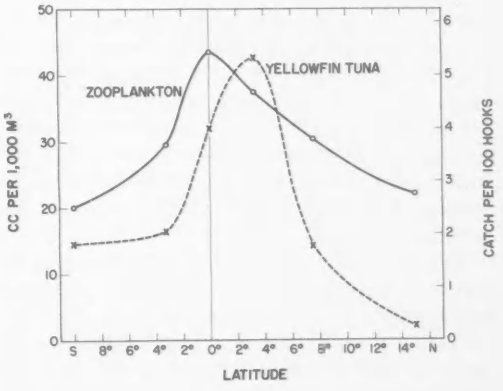

FIGURE 25.—Relative north-south displacement of zooplankton and yellowfin tuna. (Adapted from King and Hida, 1957.)

Associated with the longitudinal variations in average catch rates, the distribution of yellowfin tuna on a meridional plane appears to differ with latitude (Figure 24). In the extreme east (long 120°W), where enrichment is low, abundance of yellowfin tuna is also low and there is little evidence of increased abundance associated with the equator. Farther west (long 130°W) the abundance of yellowfin tuna is higher, and the expected peaking under prevailing southeast trades appears north of the equator. In the center (about long 150°W), where enrichment is thought to be highest and southeast trades predominate, abundance is high and centered well north of the equator. In the west, where enrichment is low and northeast trades are predominant, abundance of these tuna falls off and their distribution center is at or slightly south of the equator.

Discussion.—The available physical measurements, e.g., drogue movements and longline drifts, suggest that the northward movement from the equator is of considerable importance relative to the westward motion, and this conclusion is at variance with the results, based on ship's logs, depicted on either pilot charts or other summaries, such as our Figure 5.

As discussed in earlier sections, northward displacement of tuna with respect to plankton (Figure 25) is attributed to the time lag in the development of tuna forage, for during this period the waters are moving in a northerly direction. This northward displacement appears perfectly logical, but if so, and if the westerly flow is greater than the northerly flow, as we have generally assumed, the peak of tuna abundance should be displaced well tc the west of the zooplankton peak.

The available data (Figure 23) give little or no evidence of westerly displacement of the tuna peak relative to the zooplankton peak. This observation, coupled with empirical measurements showing that the northerly component of flow is vigorous and that the phosphate distribution is heterogeneous, makes it difficult to accept the earlier concept of an overriding western element of flow. The model, elaborated in the previous sections, that is consonant with all the evidence regards this portion of the South Equatorial Current from the equator to lat 5°N and long 120°W to 180° as comprising a series of homologous, parallel, northwesterly transport systems (Figure 19).

Temporal Variation

Variations in enrichment and distance from the source of enrichment were advanced as explanations for north-south and east-west variations in the abundance of yellowfin tuna in the region north of the equator. Most of the north-south distributions were readily reconcilable with temperature, phosphate, and plankton fields. The east-west distributions can also be explained in the same general terms, but the arguments are somewhat weaker, because the sampling program gave first priority to elucidating the distribution along the north-south axis. As a final step we propose to show that even the temporal variations in yellowfin tuna can be explained within the same framework as the spatial variation.

Murphy and Shomura (1953b) pointed out that during seasons or in areas dominated by the southeast trades yellowfin tuna tend to be concentrated north of the equator and that during periods of variable or northeast winds they tend to straddle the equator (Figure 26). This finding is consistent with the hypothesis, because either light, variable, or northeast winds should reduce the northward motion of water from the equator.

Averages such as those in Figure 26 may be misleading simply because the sampling has not been well stratified. Furthermore, although there are climatological seasons along the equator, they may frequently be altered or obscured by short-term changes to the extent that during a given year the "seasons" may not materialize. Because of the few meteorological observations in the area under consideration, it is difficult to evaluate the years in which we fished in terms of the normal. For these reasons, we evaluate the temporal changes in fish catch along a meridian in terms of the environment prevailing at the time of the catches, thus overcoming the lack

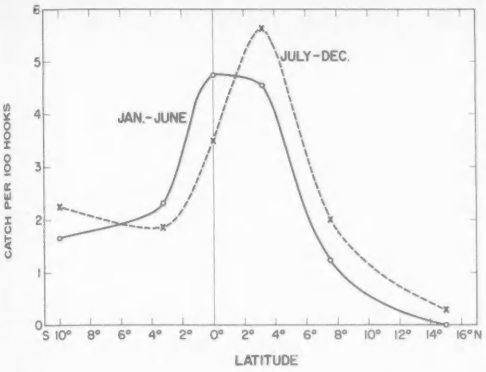

FIGURE 26.—Variation in yellowfin tuna catch with the current system for the two 6-month periods, January-June, a period with northeasterly or light and variable winds, and July-December, a period of prevailing southeasterly winds (in the equatorial central Pacific). (Adapted from King and Hida, 1957.)

of continuity of measurements of the fish and the environment.

To effect this type of analysis we must use some property in the environment that is consistently measured at each fishing station. Atmospheric data, such as winds and water temperature, are available. Winds are not suitable, because they are not conservative and because theory holds that there is a considerable lag between wind action and the response of the fish. Water temperature is more promising, since it is relatively conservative and is also a property of the immediate environment of the fish.[5]

In effect the study becomes limited to an analysis of variation along separate meridians or groups of adjacent meridians, because the water on widely spaced meridians is in all likelihood different with respect to origin and properties, such as the temperature-phosphate ratios. Furthermore, we have restricted the analyses to the zone north of the equator (lat 1°-5°N), where sampling was most intensive and where the theory of circulation is most advanced (Cromwell, 1953). The immediate vicinity of the equator is avoided on the basis of possible complications arising when this site of upwelling is considered and the unknown influence of the easterly flowing undercurrent.

Defining the geographical unit to be used in the time variation analysis as a single longitude or immediately adjacent longitudes between lat 1° and 5°N permits the development of a hypothesis. Wind action causes upwelling at the equator and a northward movement of upwelled water. This water, which might be termed "new," is cold, high in phosphate, high in plankton, and low in yellowfin tuna abundance. The meridional sections indicate that after it moves north, away from the possibility of further enrichment, it warms; phosphate declines, presumably from use; zooplankton declines, presumably from grazing; and yellowfin tuna abundance increases, presumably because the tunas congregate to feed on the forage organisms responsible for the decline in zooplankton. Water that has reached this final stage can be termed "mature."

This same reasoning can be applied to temporal variation in water temperature in places removed from the site of upwelling, i.e., the zone between lat 1° and 5°N. In this zone, the presence of cooler water must mean that the wind-driven northward movement was or is more vigorous and that the water there has been more recently enriched and has been in the euphotic zone for a shorter period of time. Consequently, it should contain more phosphate, more plankton, and fewer yellowfin tuna. Warmer water must have been longer in the euphotic zone, perhaps the result of a slowing of the wind circulation, and should contain less phosphate, less plankton, and more yellowfin tuna.

Phosphate.—If the hypothesis outlined above is correct, the concentration of phosphate in the ocean water north of the equator should be less in warmer water than in colder water, without regard to the time of sampling or place of sampling, providing consideration is restricted to the zone between upwelling and the Countercurrent

[5] It might be argued that surface temperature does not represent any substantial body of water. Fortunately, in the zone north of the equator the surface temperature is generally representative of the entire mixed layer, providing the effect of diurnal heating is suppressed. This has been done by using temperatures measured at about 9 m below the surface.

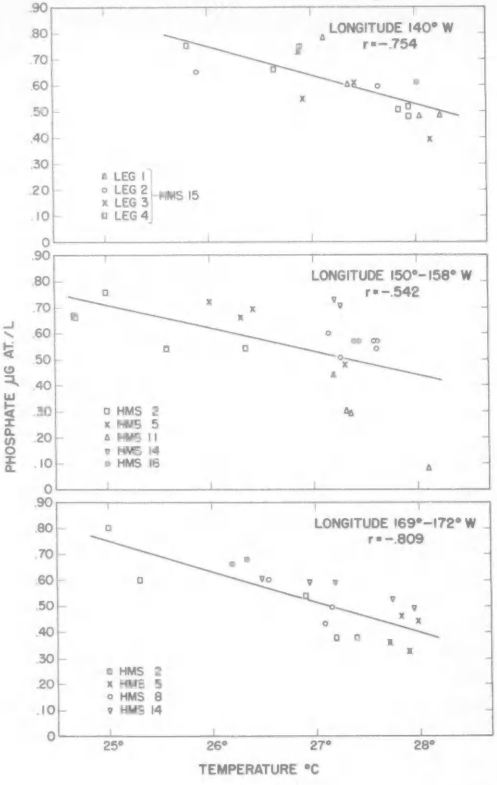

FIGURE 27.—Relations between temperatures and inorganic phosphate between lat 1° and 5°N.

and also providing single or closely adjacent longitudes are considered.

Unfortunately, there is not enough material available for a rigorous examination of surface temperature-phosphate ratios. The available data (Figure 27) between lat 1° and 5°N behave in a manner consistent with the hypothesis. Along each longitude is the expected negative regression with respect to temperature. The heterogeneity among longitudes is indicated by the reduced value of r (Table 3) when all data are considered together.

Zooplankton.—The relation between temperature and zooplankton should theoretically be a curve skewed to the right, for time should elapse between enrichment and peaking of the copepods that form the bulk of the catches. We already know, however, that the peak of zooplankton is coincident or nearly so with the center of upwelling, and since we have restricted ourselves to the zone north of the upwelling (lat 1°-5°N), we should expect to find only the descending limb of the curve.

The plots in Figure 28 indicate a significant negative relation between temperature and zooplankton, though the relation is not as striking as that between temperature and phosphate. Some of the variability may be attributable to sampling errors and some to systematic errors, such as day-night variation. As in the instance or the phosphate, the values of the correlation coefficients are higher (except for long 140°W) for the individual sections than for the data as a whole (—0.472, —0.718, —0.679 versus —0.567 for all data).

TABLE 3.—Relation of temperature to phosphate in the zone of lat 1° to 5°N[1].

Longitude	Number of sections	Number of paired observations	Correlation coefficient (r)	Probability
140°W	4	17	—0.754	<0.01
150°-158°W	5	22	—0.542	<0.01
169°-172°W	4	19	—0.809	<0.01
180°	1	5	—0.833	>0.05
All observations	14	63	—0.377	<0.01

[1] Data from Cromwell (1954), Austin (1954a, b), and Stroup (1954). Each temperature and phosphate measurement is from the Nansen bottle immediately below the surface bottle, generally at about 10 m.

Yellowfin tuna.—We have shown that maturity of the water, as indicated by the temperature of the mixed layer, appears significantly related to the amount of dissolved nutrients (phosphate) and the amount of zooplankton. It remains to project this reasoning up the trophic levels to yellowfin tuna. Probably one or more trophic levels must intervene between the zooplankton sampled and tuna, for King and Demond (1953) showed the zooplankton to be mainly copepods, and Reintjes and King (1953) showed that, although yellowfin tuna consume a variety of organisms, the bulk of their diet is composed of squid and fish.

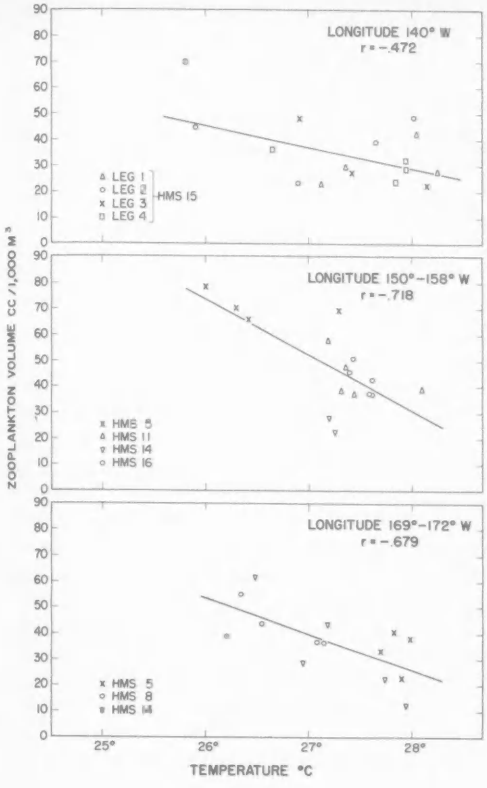

FIGURE 28.—Relation between temperature and zooplankton abundance between lat 1° and 5°N.

In attempting to specify the expected relation between yellowfin tuna and water maturity (temperature), it is helpful to start with the tuna and work back through the trophic levels. The tuna are highly motile and are capable of concentrating where food is most abundant. That is, they are not restricted to development in situ in a mass of water. To a lesser extent some of their food organisms (the larger squid and fishes) are undoubtedly able to concentrate in favorable areas that they discover either by following gradients or by random movements. It seems extremely unlikely, on the other hand, that the members of the next lower trophic level (organisms that feed on the small zooplankton) are capable of long migrations.

If this intermediate link is incapable of migration, it must develop in situ; it must be, at least indirectly, responsible for grazing down the "net zooplankton" which we measure, and because of the time needed for growth, it must reach a climax at some time after the zooplankton. Thus, we expect the forage for tuna to keep improving for some time after the zooplankton has reached its maximum development.

Since the water is warming during this period, there should be a positive relation between temperature and yellowfin tuna abundance until the water reaches senescence, at which point further increases in temperature should be accompanied by a decline in yellowfin tuna abundance. It appears, however, that actual senescence is never attained, at least in the portion of the system under study (long 120°-170°W). Instead, water probably is withdrawn from the system through convergence and possibly by the Countercurrent before reaching senescence, or even possibly before reaching maturity.

When fish catches are plotted against temperature (Figure 29), a striking relation is shown between maturity of the water (as measured by temperature) and abundance of yellowfin tuna. The measure of abundance of the tuna requires some explanation. As shown by Murphy and Elliott (1954), the catch at a single longline station is subject to very wide sampling errors—so wide in fact that any relations between catch and variables in the environment are likely to be poorly defined. For this reason the several catches in the zone of lat 1° to 5°N, during a single crossing, are considered as a unit. This treatment, in addition to suppressing sampling error, also has the advantage of directing attention to a zonal situation rather than to a point in the ocean, thereby eliminating the possible effect of other regressions along a meridional section. The temperature index parallels the tuna index in that it is also the average surface temperature over the lat 1° to 5°N zone.

Returning to the temperature-yellowfin tuna regressions, the steep slopes on long 120° and 130°W suggest a positive relation between maturity and catch. At long 148° to 155°W the

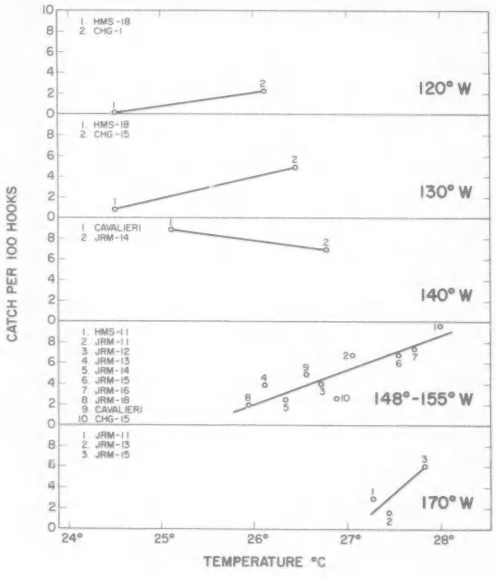

FIGURE 29.—Relations between yellowfin tuna catch and surface temperature at several longitudes for the zone lying between lat 1° and 5°N.

relation is striking and highly significant, and finally on long 170°W the positive relation is again suggested. Thus, with the exception of long 140°W, all of the fish catch data agree with the hypothesis that time variations can be explained in terms of the maturity of the water and that variations in the biota can be estimated by water temperature in this region.

The single exception (long 140°W) appears atypical in other respects. Good catches of tuna were obtained in relatively cool water, but the fishing evidently coincided with a time of rapid change; a few days after the good fishing the water cooled further and the fishing became poor. Thus, the good fishing occurred during a change from environmental conditions associated with good fishing to those associated with poor fishing. During such transitions we might expect irregularities in the relation between water maturity and catch.

The fish catches and temperatures at long 148° to 155°W plotted against time from 1951 to 1954

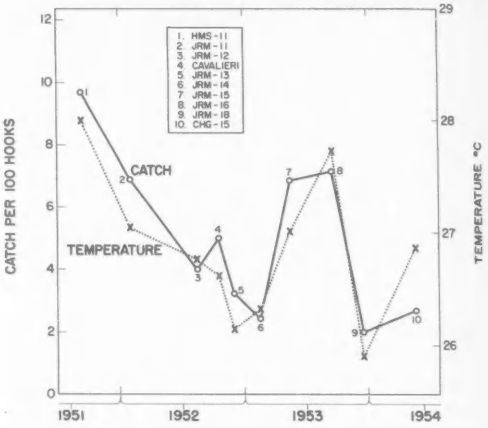

FIGURE 30.—Temperatures and fish catches between long 148° and 155°W plotted against time, 1951-54.

(Figure 30) reveal the basic relation shown in Figure 29. Generally cooler water and poorer fishing are indicated, however, in 1951-54. Superimposed on this trend is a suggestion of rising temperatures during the first half of each year and falling temperatures during the second half. These bear some resemblance to the average trends given in Table 2, but, insofar as these data are adequate, a long-term trend to cooler water appears to have almost completely suppressed the seasonal trend during 1952, thus pointing up the difficulties attending "seasonal analysis" in the equatorial area.

Temperature profiles.—It is instructive to examine the shape of the several meridional surface temperature profiles at long 148° to 155°W, because the average temperature that was compared with yellowfin tuna abundance tends to obscure certain important features. The several profiles in Figure 31 suggest that a variety of situations exists.

Two of the profiles (panel A) show relatively cool water from the equator to at least lat 4°N. This "flat" feature at low temperatures suggests very active upwelling and a northward displacement of immature water; therefore, it is not surprising that these two transects are associ-

ated with the lowest catch rates shown in Figures 29 and 30.

A second group of three profiles (panel B) has in common cool water at the equator and a steep gradient rising from south to north. This steepness of the gradients also suggests active upwelling and northward movement, and the average low water temperature implies the presence of immature water. Like the two profiles shown in panel A, these three are also associated with poor catch rates.

The profiles in the last group (panel C) show relatively little gradient, at least from lat 1.5° to 5°N. Such "flat" profiles at high temperatures should arise if upwelling and northward movement of water has slowed down, possibly in response to a shift from southeast to northeast winds or simply a marked decline in wind force. The four high catch rates shown in Figures 29 and 30 were obtained during these four periods.

The nature of the sequence of events leading to a relatively high abundance of yellowfin tuna can be inferred from the temperature profiles. First a body of enriched water should be created, and this body of water should be permitted to mature relatively undisturbed; that is, the north-south system should be slowed down. The distribution of the winds (Figure 20) suggests that such a sequence of events is most apt to occur in the central portion of the area (long 140°-160°W). In the east, southeast trades of high velocity persist during most of the year, possibly creating a south-to-north circulation with attendant convergence of such vigor that the water rarely matures in terms of tuna forage production. In the center, the southeast trades still have the substantial velocity needed to induce upwelling, but their frequency is only about 50%, suggesting there is frequently an opportunity for the water to mature. In the far west, neither

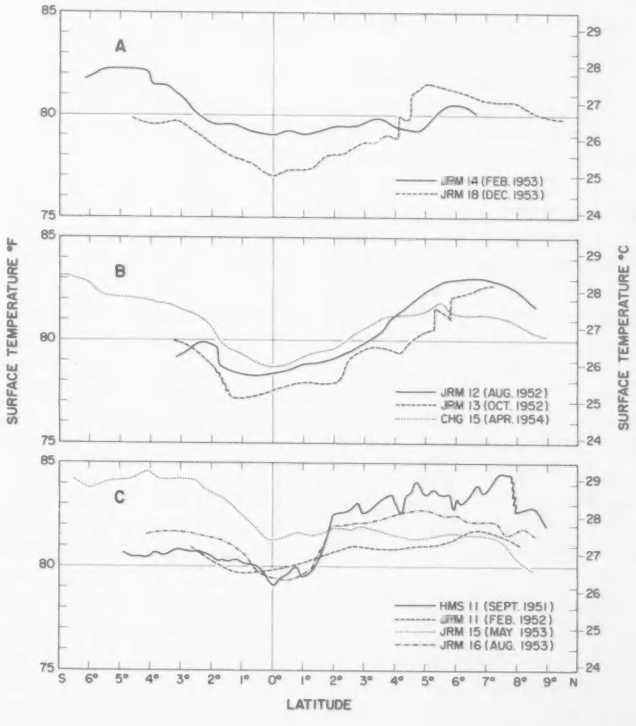

FIGURE 31.—Surface temperature profiles on longline fishing cruises along long 148° to 155°W. A. Low temperatures between lat 1° and 5°N. B. Low temperatures and a steep north-south gradient between lat 1° and 5°N. High temperatures between lat 1.5° and 5°N.

the velocity nor the frequency of the southeast trades appear high enough to create substantial bodies of enriched water north of the equator.

We now have two processes that might account for poor yellowfin tuna fishing in the east and west and good fishing in the center. The one, involving the wind pattern just described, rests on the assumption that if enriched water is to result in a dense population of yellowfin tuna, it must remain relatively undisturbed in the euphotic zone long enough for a forage population to develop. The other, discussed in the section on nutrients, is based on the vertical distribution of phosphate at various longitudes along the equator. Phosphate distribution, when viewed against the wind distribution, suggests that the absolute amount of enrichment might be greatest in the center of the area, and it is in this area that the enriched water appears to have a reasonable chance to mature before convergence. The two processes are independent but interact in a way consistent with the occurrence of the best yellowfin tuna fishing in time and space.

In addition to variation in the catch rates at a given longitude, there have been changes in the meridian of the best catches. For the year 1953 there are enough records to illustrate this phenomenon (Figure 32). Such shifts are in harmony with the present theories of the factors controlling yellowfin tuna abundance. The yellowfin tuna are highly motile, and we expect them to be most abundant where conditions best suit them. For instance, if upwelling is too vigorous over the area from long 120° to 150°W and less vigorous farther west, conditions should be better in the west. This situation may well explain the pattern in May-June of 1953 (Figure 32). On the other hand, in August 1953 yellowfin tuna seemed to be most abundant near long 155°W; this distribution would be expected if strong upwelling and northward displacement at some time in the past was followed by a period of relative quiet.

These deductions are difficult to test critically, i.e., it is difficult to make a critical comparison between fish catch and some factor in the environment such as temperature because of the heterogeneity of the water when considering the equator as a whole. However, there is a suggestion of an association in our data: During February-April 1953 (Figure 32) the catch was better on long 140°W than on long 150°W, and at the same time the mixed layer was about 0.5°C lower on long 150°W than on long 140°W. This is a reversal of the average trend (Figure 23) and could only have resulted from the water at long 150°W being more recently affected by upwelling and northward displacement than that at long 140°W. In perfect agreement with our hypothesis, this relatively newer water at long 150°W had a smaller population of tuna.

In summary, it has been possible to develop a functional hypothesis consonant with the mechanics of the equatorial system that can logically account for all, or nearly all, of the major observed variations in the abundance of the large deep-swimming yellowfin tuna. The theory successfully embraces variations in catch rate in respect to time and in respect to space. Since the root of the system lies in the winds, it should be possible eventually to anticipate the variations in the yellowfin tuna population by examining variations in the wind regime.

SURFACE TUNAS

The principal methods we have used to sample surface tunas are surface scouting and trolling. Live-bait fishing has also been used occasionally. These are the same methods used to locate tunas by the several live-bait and purse-seine fisheries in the Pacific.

Each of these survey methods has inherent weaknesses that cannot be estimated quantitatively. Perhaps the greatest difficulty in surface sighting lies in the state of the sea. The central Pacific is nearly always choppy, practically precluding detection of schools at the surface unless they are breaking water or are accompanied by feeding birds, e.g., in our experience 85% of all schools were first sighted through the accompanying "working birds." In effect, we do not see tuna unless their presence is marked by birds; this relation casts doubt on the census method. The problem, however, may not be as serious as it seems, for the association between birds

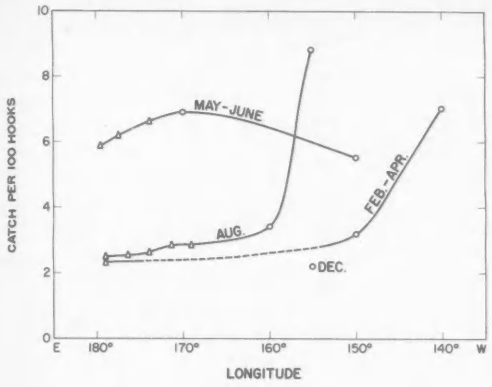

FIGURE 32.—Catch rates of yellowfin tuna by longitude and by time of year (1953).

and fish may have a firm biological basis in that feeding tunas, by driving small fish and squid to the surface, appear to be an important factor in making food available to birds.

The observed behavior of working bird flocks substantiates this contention. A bird flock may be first seen when it is feeding over a school, the birds excitedly circling close to the sea surface and frequently plummeting into the sea to capture prey. Subsequently, the school may sound and the birds discontinue feeding, scatter somewhat, and rise to a higher elevation as though scouting for the school. As soon as the school appears again at the surface, the birds quickly assemble over it and resume feeding. This relationship suggests that the abundance of pelagic predators such as tuna may directly affect the abundance of birds by controlling the amount of food available to them. Insofar as this is true, bird abundance should form an index of fish abundance.

On the other hand, it is difficult to discount completely the possibility of introducing error through the use of birds as an indicator of fish, for the frequency of sightings of both birds and fish is everywhere parallel (Murphy and Ikehara, 1955), and it seems unlikely a priori that the populations of both need always be parallel. For instance, birds and fish are seen more frequently around islands than far at sea. Oceanic birds nest on land, thus tending to make islands focal points for their populations; but, is the vicinity of land also a focal point for tuna schools? Perhaps so, for nesting birds have an even greater demand for food than wandering birds, and thus the magnitude of their concentrations around islands must be based on the food supply too and, to the extent that they obtain their food over schooling tunas, on the abundance of schools of surface tunas.

Aside from the problem of just what surface sightings mean in relation to tuna abundance, the validity of conclusions based on relatively scanty sampling of so vast an area as the central Pacific (Figure 3) can be questioned. The only available test, a comparison of sightings from the Laboratory's vessels with the seasonal changes in Hawaiian commercial landings (Figure 33), shows that in general a seasonal prediction based on our relatively scanty observations would have been borne out by the commercial catch. Thus, it appears that rather limited scanning of the sea can yield results compatible with those from a very large amount of effort (the commercial fishery).

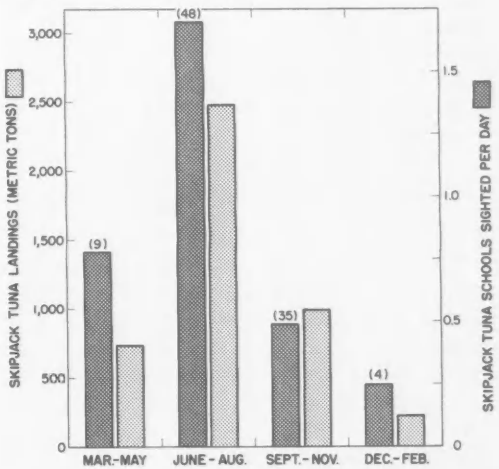

FIGURE 33.—Comparison between average Hawaiian skipjack tuna landings (1950-52) and surface sightings of skipjack tuna schools (number of schools sighted noted above bar diagrams) from research vessels in the Hawaiian Islands area (data from Murphy and Ikehara, 1955).

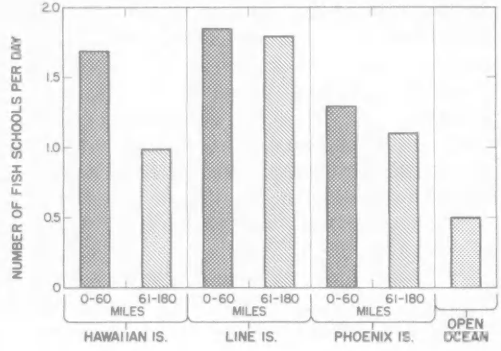

FIGURE 34.—Frequency of sighting fish schools in various zones (distance from land) and areas of the central Pacific (data from Murphy and Ikehara, 1955).

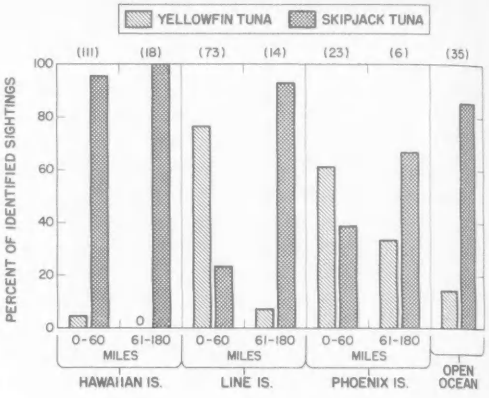

FIGURE 35.—Relative occurrence of yellowfin and skipjack tuna schools at various distances from land. Number above bar diagram represents total number of schools sighted.

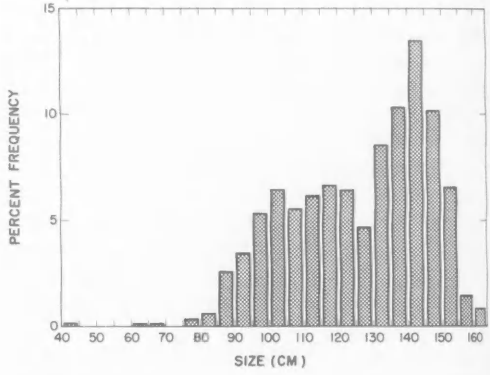

FIGURE 36.—Length frequency of longline-caught yellowfin tuna at all insular fishing stations (within 96.5 km of land).

Systematic trolling is a well-known and established method of quantitatively surveying the availability of surface fish. The only serious flaw in our data has been the difference in availability to troll lures of the principal surface species, skipjack and yellowfin tunas (Murphy and Ikehara, 1955). For instance, near the Hawaiian Islands half as many yellowfin tuna were taken by trolling as skipjack tuna, whereas other measures, e.g., the commercial catch (June, 1951), suggest that there are only about one-tenth as many yellowfin tuna as skipjack tuna.

DISTRIBUTION OF SURFACE TUNAS RELATIVE TO LAND

The general abundance of surface schools depicted in Figure 34 shows that schools are seen several times more frequently near islands than in the open ocean. This can be interpreted as merely indicating the abundance of birds, but, as is shown later, it is also possible to regard the islands as creating in their vicinity special conditions that are conducive to the occurrence of surface-schooling tunas.

In addition to differences in abundance between island waters and the open ocean, species composition appears to shift, in that yellowfin tuna schools tend to favor the vicinity of islands (Figure 35). About 47% of all schools sighted were identified as either yellowfin tuna or skipjack tuna, a small percentage were identified as other species, e.g., the common dolphin, and the rest were unidentified (Murphy and Ikehara, 1955). The relative percentages of the two important species plotted in Figure 35 show very clearly that (1) skipjack tuna are dominant in the Hawaiian Islands area and in all offshore areas, and (2) in each instance relatively more

yellowfin tuna schools are found near land than offshore. In fact, in the Line and Phoenix groups yellowfin tuna appear to have replaced skipjack tuna near land. Thus the presence of land seems to create favorable circumstances for the occurrence of tuna schools in general and yellowfin tuna schools in particular.

This distribution of yellowfin tuna in relation to land is also borne out by longline catches of yellowfin tuna near land and offshore. Figure 36 shows that when longline gear is fished near islands it catches more of the smaller yellowfin tuna that compose surface schools than it does when fished offshore (compare Figure 36 with Figure 4). This increased abundance of small yellowfin tuna near islands is also shown in Figure 37, which indicates that about half of the increase in longline catch rates near shore stems from the addition of small fish to the catch. Furthermore, the increase in small fish in the longline catches is roughly proportional to the increase in the rate of surface sighting of this species near land. A final indication that small yellowfin tuna are more abundant near land is that surface trolling took 10 times as many yellowfin tuna per unit of effort within 96.5 km of land as beyond that limit (Murphy and Ikehara, 1955). Since all three sampling methods—longlining, sighting, and trolling—clearly show small surface yellowfin tuna to be more abundant near land, we conclude with little or no reservation that the occurrence of young yellowfin tuna in the central Pacific is intimately related to the presence of land.

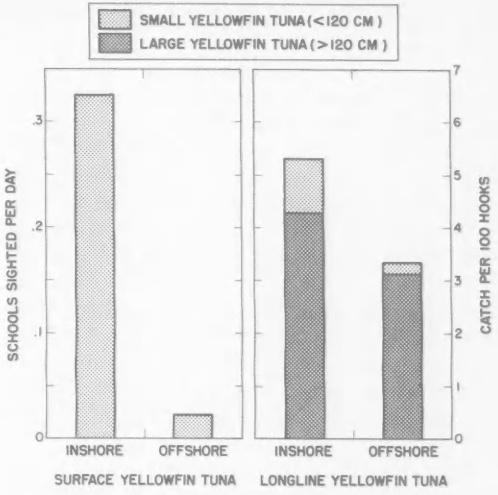

FIGURE 37.—Relative occurrence of schooling yellowfin tuna in surface sightings and longline catches for inshore and offshore areas.

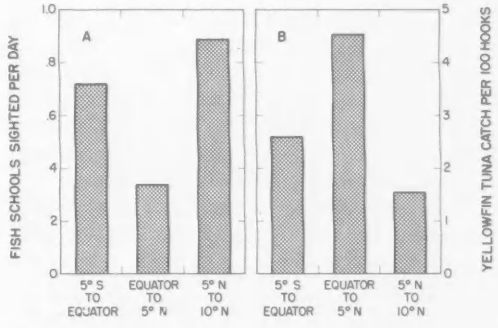

FIGURE 38.—Latitudinal distribution of surface tuna schools and deep-swimming yellowfin tuna. A. Sightings of surface tuna schools in the open ocean (Murphy and Ikehara, 1955). B. Yellowfin tuna catches from fishing stations more than 96.5 km from land and between long 140° and 170°W.

OCEANIC DISTRIBUTION

Despite the low average abundance of tuna schools in the open ocean (Figure 34) certain areas or zones appear to support populations with a density comparable to that of the island areas. Over most of the central Pacific our sampling is not adequate to focus attention on particular areas except in the central portion of the study area (long 140°-170°W). Here, there are enough days' observations to make meaningful zonal comparisons (Figure 38A). It is apparent that the number of schools sighted in some of these zones is nearly the same as for the Hawaiian Islands area, e.g., 0.9 school seen per day in the Countercurrent (Figure 38A, lat 5°-10°N) and 1.7 near the Hawaiian Islands (Figure 34). Considering how far removed these zones are from land, we might conjecture that considerably more schools would have been sighted if

more birds had been available. Such pelagic populations as these must represent a vast untapped resource, judging from the 5,000 tons or so taken annually in a limited area around the Hawaiian Islands (June, 1951).

The distribution of oceanic schools is at variance with the distribution of deep-swimming yellowfin tuna (Figure 38B), the most striking differences being the high density of schools in the Countercurrent (lat 5°-10°N) and south of the equator. In fact, the distribution of surface schools is almost the inverse of the distribution of deep-swimming tunas. This apparent inverse relation poses a serious problem, for a priori we would expect surface schools to respond to the equatorial enrichment in the same manner as the deep-swimming tunas.

The problem can be approached by considering the environmental factors that make it possible for an area to support large numbers of surface schools. The obvious one that comes to mind is the standing crop of forage, as indicated by zooplankton. We have already indicated, however, that zooplankton tends to peak at the equator (Figure 25), and thus food supply as indicated by the standing crop of zooplankton does not account for the north-south distribution of surface fish. In a possibly parallel situation, King and Hida (1954) found little or no more zooplankton around the Hawaiian Islands than in the North Pacific Current and were unable to account for the population of skipjack tuna around Hawaii on the basis of the standing crop of zooplankton.

A suggestion of an important environmental factor controlling the abundance of skipjack tuna was given by Robins (1952), who found a positive association between skipjack tuna troll catches and temperature discontinuities or "fronts." The circulation associated with fronts involves horizontal convergence and sinking, according to Cromwell (1956). This type of movement could act to concentrate organisms, particularly those that float or can actively resist sinking. Fronts might act as modifiers of the average standing crop by altering its distribution in space so that fishes can more effectively forage.

The effect of fronts on the distribution of forage might account for the abundance of schools near islands. An island mass in a moving ocean current must set up patterns of "frontlike" circulation cells and eddies, as has been shown for the Hawaiian Islands (McGary, 1955). These features, although perhaps not increasing the basic supply of food, should concentrate some of it so that fish can feed more efficiently.

In an effort to determine whether this same mechanism could be offered as an explanation of the irregular distribution of surface schools in the equatorial region (Figure 38), we determined the frequency of temperature irregularities at the sea surface, confining ourselves to the best-sampled zones, i.e., lat 5°S to 10°N, long 140° to 170°W. The frequency of occurrence of temperature irregularities or "fronts" was estimated from thermograph traces made while the ships were crossing the equatorial system in a north-south direction. An irregularity was simply defined as a temperature change that was completed during 15 min or less when the ships traveled at a speed of about 8 knots, i.e., long, even temperature clines were not considered. If the temperature rose (or fell) quickly to a new level, this was counted as one "front." If it both rose and fell during any interval, it was counted as two "fronts," providing the rise and the fall each took no more than 15 min.

An inquiry can logically be made into the relation of wind velocity to the number of such fronts, for on calm, hot days there may be many irregularities caused by convection currents set up by diurnal heating. A plot of wind force against the number of fronts in unit time, however (Figure 39), suggests that we are dealing with phenomena that are independent of the immediate wind stress and heating.

When we compare the rate of crossing fronts with the rate of sighting surface schools, we find a remarkable correspondence (Figure 40), enabling us to advance the same explanation for differences in abundance of surface schools among different areas of the open ocean and between the vicinity of islands and the open ocean. The responsible feature of the environment, the "front," meets the test of biological and physical logic, for temperature fronts are symptomatic of horizontal movement of water toward the dis-

continuity and sinking at the discontinuity, a mechanism that should concentrate certain types of tuna forage or food for tuna forage.

We are still confronted with the basic difference in the distribution of surface and deep-swimming tunas (Figure 38), though we have logically advanced two hypotheses that seem adequate to explain each distribution pattern when the problems are considered independently, i.e., basic enrichment and northward drift of upwelled water in the instance of the deep-swimming tunas, and "fronts" in the instance of surface schools. An entering wedge is offered by the difference in social behavior between the deep-swimming and surface schools.

Sette (1950), in discussing mackerel, proposed that schooling was advantageous to any predator feeding on prey that was aggregated. In fact, the very existence of schools of carnivores would seem to require schools or aggregations of prey, for if prey were distributed at random, it could be most effectively harvested by pursuit and capture of individuals by individual predators. In other words, where we find scattered prey we should expect scattered predators. In the present instance, where we have a mechanism ("fronts") for concentrating prey, we find surface schools, and where the mechanism is not present we do not find the schools. The deep-swimming tunas, on the other hand, are not aggregated into large, compact schools (Murphy and Elliott, 1954) and so might be expected to use more or less scattered forage organisms more efficiently, and the distribution of such tunas might be expected to conform more closely to the mean distribution of forage, rather than the distribution of concentrating mechanisms.

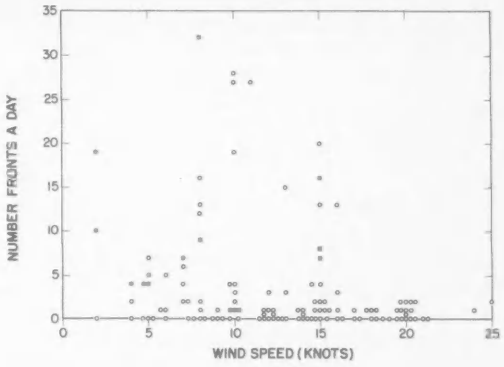

FIGURE 39.—Daily frequency of fronts as a function of daily noon wind speed (lat 5°S-10°N, long 148°-170°W).

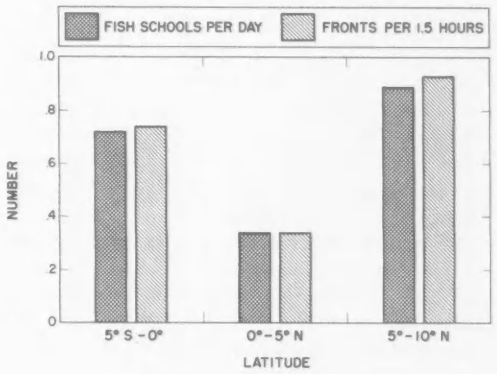

FIGURE 40.—Rate of crossing temperature discontinuities and rate of sighting fish schools near the equator (vessel speed about 8 knots, vessel course always north or south). Longitudinal limits 140° to 170°W.

SUMMARY

1. Surveys of tuna populations and environmental conditions were made in the equatorial central Pacific in 1950-53.

2. Tunas were sampled by longline, trolling, live-bait fishing, and sighting from the bridge of a research vessel.

3. The longline was used more than the other methods of fishing, because it was the most consistently productive sampling method, particularly on the high seas.

4. Tunas, especially yellowfin tuna, may be divided into two groups, small surface-swimming tunas and large deep-swimming tunas.

5. On the basis of longline catches, deep-swimming yellowfin in the central Pacific were most abundant near the equator.

6. Deep-swimming bigeye tuna were nowhere as abundant as yellowfin tuna. Two tongues of

relatively high bigeye tuna catches occurred in the equatorial Countercurrent.

7. Deep-swimming albacore were most abundant in the southwestern area, e.g., around lat 5°S, long 170°W.

8. Skipjack tuna were found over the entire area.

9. Deep-swimming yellowfin and bigeye tunas were larger in the east (e.g., 120°W) than in the west (e.g., 130°E). The reason for this difference is obscure.

10. Analyses of tuna catches and properties of the environment in a meridional plane revealed the following: There is upwelling and enrichment at the equator; the upwelled water is displaced northward; zooplankton peaks are at the center of upwelling, apparently because of a time lag in the development of tuna forage.

11. The water flow near the equator differs from the classical concept in that empirical measurements suggest the northward motion is of the same magnitude as the westward motion. Thus the South Equatorial Current just north of the equator should be regarded as a series of parallel, homologous, northwesterly flow systems.

12. Variation in surface temperatures at the equator is a function of surface winds, through alteration of the rate of upwelling.

13. Interaction of geographical variation in the vertical distribution of nutrient salts and the geographical distribution of wind stress cause the greatest enrichment through equatorial upwelling to occur in the central area (near long 140°W).

14. In the area surveyed, between long 120°W and 180°, both zooplankton and yellowfin tuna were most abundant near the center of the area (near long 150°W).

15. When northeast trades prevail, yellowfin tuna seem most abundant south of the equator; during southeast trades, north of the equator; and during variable winds, the peak abundance straddles the equator.

16. Between the equator and the Countercurrent the presence of colder water is associated with more phosphate, more zooplankton, and fewer yellowfin tuna. Warmer water is associated with less phosphate, less zooplankton, and more yellowfin tuna. We believe that these differences are a reflection of the time lapse since enrichment and that variations at a geographical locality are in response to variations in wind flow that affect the rate of upwelling.

17. There are suggestions of annual seasonal variations in the abundance of yellowfin tuna near the equator, but these may be masked by longer term secular trends.

18. Changes in abundance at a point on the ocean may result from east-west shifts in the yellowfin tuna population as well as north-south shifts, or simply general dispersion from or concentration at that point. All of these variations may be logically attributed to variations in the enrichment at the equator, brought about by variations in the winds.

19. Surface tunas are seen more often close to land, possibly because more birds are present there.

20. In the equatorial central Pacific, yellowfin tuna tend to predominate in surface schools close to land and skipjack tuna far from land.

21. Near the equator, the abundance of surface schools does not seem to coincide with the peaks in abundance of the deep-swimming tunas. Food concentrating mechanisms appear to be more important than basic food supply in affecting the local abundance of surface-swimming schools.

ACKNOWLEDGMENTS

We take great pleasure in acknowledging Oscar E. Sette for the leadership and guidance provided the authors during the investigation of the tuna resources of the equatorial central Pacific; the investigation upon which this report is based. As Area Director of the Hawaii Area from 1949 to 1955, O. E. Sette initiated this tuna-oceanography study of the vast unknown equatorial waters in 1949.

Practically the entire scientific staff of the former Bureau of Commercial Fisheries Biological Laboratory, Honolulu, helped collect the data at sea during the 1950-53 period. In the Laboratory, Jean S. Halling and Richard N. Uchida were responsible for much of the processing of biological data. In addition to O. E.

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O. E. Kerns and Frank Williams reviewed the manuscript.

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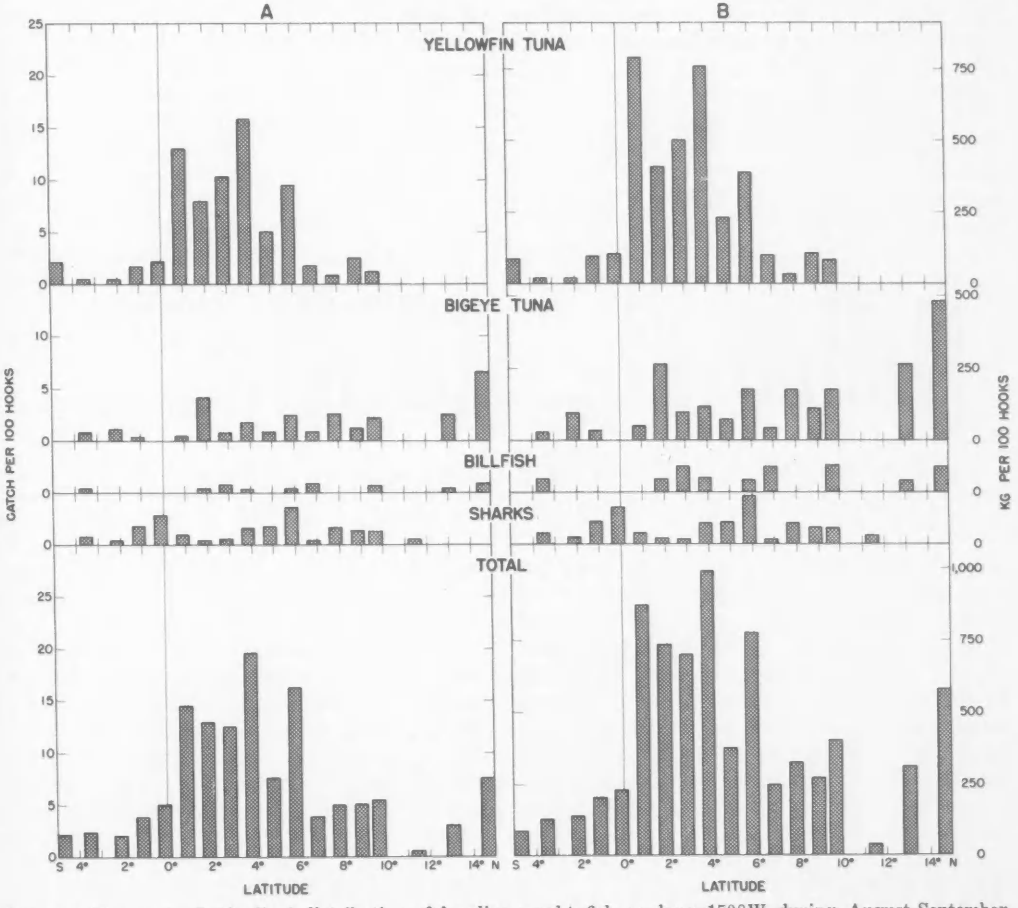
APPENDIX A

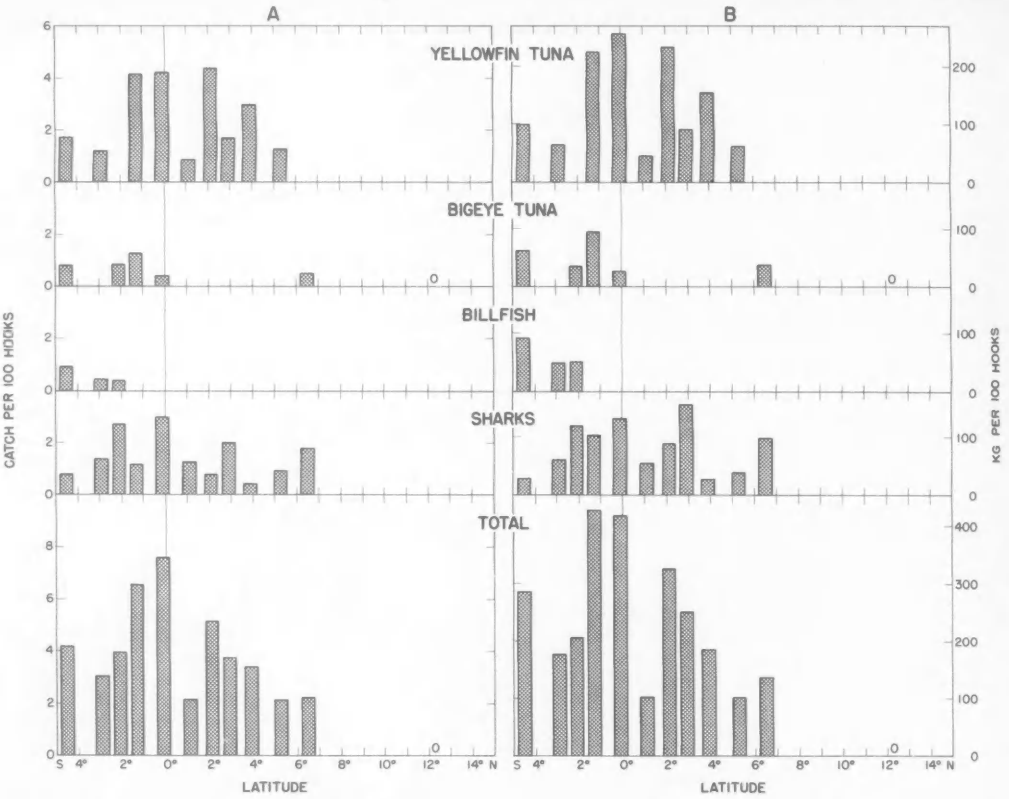
VALIDITY OF YELLOWFIN TUNA AS AN INDEX OF THE TUNA-SHARK TROPHIC LEVEL

Throughout this paper we have compared the distribution of tuna with the distribution of certain biological and physical properties of the environment. We have examined these environmental properties in relation to the number of yellowfin and other tuna captured per 100 hooks. This procedure could lead to misinterpretation, if the size of the individuals taken varies significantly or if the relative abundance of species within a trophic level changes with respect to time or space.

Ideally, we wish to ascertain the relative



APPENDIX FIGURE 1.—Latitudinal distribution of longline-caught fish on long 150°W during August-September 1951, a period of good fishing success. A. Number of fish per 100 hooks. B. Weight (in kilograms) per 100 hooks.



APPENDIX FIGURE 2.—Latitudinal distribution of longline-caught fish on long 150°W during January-February 1953, a period of poor fishing success. A. Number of fish per 100 hooks. B. Weight (in kilograms) per 100 hooks.

weight of fish life at a given trophic level and compare that weight with other properties of the biosphere, e.g., standing crop of zooplankton. Uniform sampling of a given trophic level, especially if it comprises several species, is difficult. In the longline, however, we have a tool that appears to sample a reasonably restricted trophic level. All of the principal species taken are definitely carnivorous, as shown by their attraction to fish baits, so this characteristic defines and restricts the "trophic level." In the present instance the trophic level is composed principally of tunas, sharks, and billfishes.

Additional information that aids in defining the trophic level stems from studies of the food habits of the fishes. King and Ikehara (1956) have shown that the yellowfin and bigeye tunas in the central Pacific essentially share a common diet of small to medium-sized invertebrates and fishes. Recent studies suggest that the same statement applies to the skipjack tuna and albacore. Most pelagic sharks taken on the longline in the central Pacific also seem to share the tuna forage (Strasburg, 1958). Large billfishes, however, appear to represent a somewhat higher trophic level. The smaller items in their diet approximately coincide with the large items in the diet of the tunas and sharks. Thus, there are good grounds for considering tunas and sharks as representatives of a restricted trophic

level, but the inclusion of billfishes is open to question.

On the subject of numbers of fish versus weight, Appendix Figures 1 and 2 depict the results of two section lines along long 150°W, one representing good and the other poor fishing. The members of each pair of panels give the same impressions. In the first series abundance is very high between lat 1° and 6°N and considerably lower to the north and south. In the second series the total abundance is much lower, but the catches definitely peak between lat 2°S and 4°N. The inclusion or omission of the billfishes, thought to represent a slightly higher trophic level than the tunas and sharks, has little effect on the major trends.

We may draw two important conclusions from the plots of number and weight. Because the trends are nearly the same, the average size of each of the component species must change little, if at all, with latitude. Even more important, it is apparent that latitudinal variations in catch are largely a function of variations in yellowfin tuna abundance, particularly between lat 5°S and 5°N, the general area in which this study has been focused. Because the yellowfin tuna is the most important species in this region, we lose little biologically and gain much in ease of understanding by restricting comparisons of the fish population and the environment to yellowfin tuna.

One flaw in these arguments for considering yellowfin tuna only is our failure to take into account the skipjack tuna, for it almost certainly belongs to the same trophic level as the yellowfin tuna. Although small yellowfin tuna are almost absent from longline catches in the oceanic areas under consideration, skipjack tuna are strongly represented. In fact the available evidence suggests they are abundant to the north of the concentration of yellowfin tuna (lat 5°-10°N). We can offer no satisfactory solution, for it is not yet possible to combine quantitatively measures of abundance of deep-swimming fishes with those of surface fishes. In our opinion, however, if it were possible to add skipjack tuna to the weight diagrams of Appendix Figure 2, there would be little change in the relative distribution of the tuna-shark trophic level near the equator.

BEHAVIOR OF BLUEFIN TUNA SCHOOLS IN THE EASTERN NORTH PACIFIC OCEAN AS INFERRED FROM FISHERMEN'S LOGBOOKS, 1960-67[1]

J. MICHAEL SCOTT[2] AND GLENN A. FLITTNER[3]

ABSTRACT

Fishermen's records of 8,059 purse-seine sets made on *Thunnus thynnus* (bluefin tuna) were examined for the period 1960-67. A total of 3,538 sets were identified as to school type. The majority of these sets were made within 90 miles of the beach off southern and Baja California from lat 23°N to 34°N. The region was divided into a northern and southern area on the basis of biological and oceanographic factors.

Significant differences were observed in the occurrence of the six most common school types between the northern and southern most areas of the fishery. The difference in occurrence of the jumping, boiling, and shining schools was related to the relative absence of red crabs (*Pleuroncodes planipes*) in the northern area and to differences in the foraging behavior of *T. thynnus* on baitfish and red crabs.

Differences in vulnerability to capture and catch per successful set were noted among the five most common daytime schools as well as with respect to time of day.

Purse-seine sets made with the assistance of airborne spotters had larger catches and a greater percentage success than did unassisted sets. In addition the percentage of a particular school type taken with aircraft assistance was inversely proportional to the visibility of the schools from the mast.

The existence of different school types in scombroid fishes has been noted by several authors. In 1931, Suzaki (as cited by Uda, 1933) recognized five types of skipjack tuna (*Katsuwonus pelamis*) schools in the western tropical Pacific. Kimura (1954) listed six types of skipjack tuna schools. To these Inoue (1959) added three additional types based on behavior and association of the tuna with animals and inanimate objects. Ogilvie (1949)[4] described 10 types of tuna schools commonly encountered in the eastern tropical Pacific. McNeely (1961) stated that the California tuna fishermen recognized several different school types for yellowfin (*Thunnus albacares*), skipjack, and bluefin tuna (*T. thynnus*). Scott (1969) described 16 different school types for the eastern Pacific tunas, listed fishermen's synonyms, and placed them into two major groups and five lesser categories on the basis of time of day, depth of occurrence, and association with other animals and floating objects.

Various attempts have been made to correlate the type of school with fishing success. Uda (1933) and Uda and Tukusi (1934) attempted to show an "index of biting" for the different school types as did Kimura (1954). Inoue (1959) correlated the percentage success of the Japanese purse seiner fleet with school types for yellowfin, skipjack, and bluefin tuna in the western tropical Pacific. Inoue's data indicated that possible differences in school size and vulnera-

[1] This work was initiated while both authors were employed in the Tuna Resources Laboratory of the Bureau of Commercial Fisheries (now the National Marine Fisheries Service, Southwest Fisheries Center) under the direction of Dr. Richard R. Whitney, then leader of the Tuna Behavior Program.

[2] Department of Zoology, Oregon State University, Corvallis, OR 97331.

[3] Bureau of Marine Sciences, San Diego State College, San Diego, CA 92115.

[4] Ogilvie, H. 1949. Description of various types of tuna schools, of behavior, methods of fishing and production possibilities in relation to pole and line fishing encountered in Central America. Inter-American Tropical Tuna Commission, La Jolla, Calif. 5 p. (Manuscr.)

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bility to capture existed among the various school types as well as between the three species.

MATERIALS AND METHODS

In order to describe the schooling behavior of *T. thynnus* in the eastern North Pacific and to relate this behavior to percentage of successful sets and catch per successful purse-seine set, California fishermen's logbooks were analyzed for the period 1960-67. Abstracts of these logs were made available through the courtesy of the Inter-American Tropical Tuna Commission.

A purse-seine set is defined as that operation in which the net is laid out around a school of fish and the bottom of the net drawn together, capturing the fish, which are then transferred to the vessel (Orange, Schaefer, and Larmie, 1957). A complete description of the fishing operation is given by McNeely (1961). For the purposes of this paper the term "school" will apply to that quantity of fish captured in a successful set of the net. No assumptions as to the configuration of the school nor the orientation of the fish within the school will be made (see Williams, 1964; Breder, 1967).

Orange, Schaefer, and Larmie (1957) made several assumptions in analyzing single set data from fishermen's logbooks, and other workers have followed (Broadhead and Orange, 1960; Whitney, 1969). These assumptions are:

1. A set of the net is made on a single school of fish.
2. Either the entire school is captured or each set captures a constant fraction of the school upon which it is made.
3. Vessel masters can estimate accurately the tonnage from individual sets of the net.

In addition, it is assumed that the schooling behavior described in ship's logs indicated the school type evident when the fish were first observed.

The average size of all schools may actually be smaller than those cited by the fishermen because small schools of 2 tons or less may be passed over by the fishermen in the hope of capturing a larger school later in the day.

In regard to the second assumption, fishermen generally agree that it is extremely difficult to "cut" a tuna school with their nets; it appears to be an all-or-nothing situation. Typically a fisherman will catch ¼ ton or less when the school is missed. These fish usually are entrapped in net folds during the pursing operation and are unable to escape with the main body of the school being set upon. The constant fraction, therefore, approaches zero. That the second assumption does not hold in every case was recognized by the original proponents (Orange, Schaefer, and Larmie, 1957). We have assumed also that the fraction of fish retained in the net from a school escaping capture is the same for all school types, as well as for all times of day; these are factors which need additional study.

Fishermen identify schools to species with considerable skill, but the system of identification is difficult to describe. Their ability to judge tonnage, however, is very good after the fish are inside the net and in full view of the mastman. The airborne spotters are extremely good at estimating school size.

Bluefin net sets were defined to be: 1) all sets in which 90% or more of the total tonnage landed was *T. thynnus*, 2) all no-catch sets in which *T. thynnus* was clearly identified as the pursued species, and 3) all sets in which it could be determined from location, water temperature, date, time, and previous and later sets by the same or other boats operating nearby that it was *T. thynnus* being sought and/or captured. Using the above criteria, we determined that a minimum of 8,059 sets were made on *T. thynnus* and 65,478 tons landed by the eastern North Pacific high seas purse-seine fleet during the period 1960-67. Of these sets, 43.9% were identified in the logbooks as to school type.

All weight references in this paper are expressed in short ton units.

SCHOOLING BEHAVIOR

The terminology of school types used in this paper is that of Scott (1969) (Table 1). *T. thynnus* exhibited 13 different types of schooling

TABLE 1.—Terms used by southern California purse-seine tuna fishermen to describe various types of tuna schools and associations (from Scott, 1969).

School fish	Associated schools[1]
Surface schools[1]	Fish and mammals[1]
Breezer	Porpoise schools
Finner	Spotters
Jumper	Spinners
Boiler, foamer, smoker, or meatball	Spotters and spinners
	Whitebelly
	Whale schools
Subsurface schools[1]	
	Shark schools
Black spot, dark spot, brown spot, green spot, or black ball	Inanimate object association[1]
Shiner	Log school
	Bait boat
Night schools[1]	
Fireball, ardura, glow spot, white spot, or flare	
Popper	

[1] These terms are used for organization of the table and are not used by the fishermen.

behavior and 12 different combinations of these to the commercial fishermen. There were differences in frequency of occurrence, size of the schools, and vulnerability to capture between the schools (Table 2). Differences in the occurrence of the school types in the northern and southern areas of the fishery were also evident (Table 3).

In order to eliminate possible bias in analyzing school size and percentage success, all sets made with the assistance of airborne spotters have been separated. The effects of airborne spotters on catch data will be discussed later in this paper.

Of the 13 school types observed, only 6 were recorded often enough (50 or more times) to warrant attention.

GEOGRAPHICAL VARIATION

T. thynnus is taken along the coast of Baja California and southern California from lat 23°N to 34°N. Occasionally fish are taken north of this area, especially in warm water years, but they are few, and seiner operations are severely limited by prevailing weather and sea conditions. The greatest percentage of the bluefin catch is made within 90 miles of shore near shoals, banks, reefs, and islands.

We have divided the area of the fishery into two major areas: that area north of lat 28°59'N and the area south of and including that same latitude (Figure 1). There is some biological basis for this division, as Punta Eugenia marks the northernmost extension of the Panamic fauna (Steinbeck and Ricketts, 1941). In addition, oceanographic and meteorological conditions also differ considerably. South of Punta Eugenia, an annual visitation of warm tropical

TABLE 2.—Catch statistics for 13 different bluefin school types and 4 different categories of combined schooling behavior observed.
[All purse-seine sets recording schooling behavior are included.]

School type	Total sets	Successful sets		Total catch (short tons)	Average catch per successful set (short tons)
		Number	Percent		
Breezers	1,871	870	46.5	17,043	19.6
Boilers	221	141	63.8	1,286	9.1
Jumpers	639	414	64.8	2,192	5.3
Black spots	137	61	44.5	1,475	24.2
Shiners	111	67	60.4	776	11.6
Foamers	7	5	71.4	104	20.8
Fireballs	397	293	73.8	4,423	15.1
Finners	7	5	71.4	45	9.0
Log	1	0	0	0	0
Whales	15	6	40.0	91	15.2
Poppers	8	6	75.0	29	4.8
White spots	7	6	85.7	58	9.7
Meatballs	3	2	66.7	40	20.0
Combined schooling behavior recorded for the following					
Breezers	96	45	46.9	837	18.6
Boilers	4	3	75.0	68	22.7
Jumpers	10	8	80.0	68	8.5
Black spots	4	2	50.0	38	19.0
Total	3,538	1,934	54.7	28,573	14.8

TABLE 3.—Catch statistics for all non-aircraft assisted bluefin purse-seine sets recording schooling behavior.

School type	North of lat 28°59'N					South of lat 28°59'N					Northern and southern areas combined				
	Total sets	Successful sets		Catch per successful set (short tons)		Total sets	Successful sets		Catch per successful set (short tons)		Total sets	Successful sets		Catch per successful set (short tons)	
		Number	Percent	Median	Range		Number	Percent	Median	Range		Number	Percent	Median	Range
Breezers	475	206	43.4	10.5	0.3-100.0	1,037	492	47.5	14.0	0.5-145.0	1,512	698	46.1	12.0	0.3-145.0
Boilers	191	114	59.7	4.0	0.3- 73.0	13	7	53.9	25.0	4.0-106.0	204	121	59.3	4.0	0.3-106.0
Jumpers	572	363	63.5	2.0	0.2- 25.0	23	16	69.6	5.0	1.0- 44.0	595	379	63.7	2.0	0.2- 85.0
Black spots	17	5	29.4	9.0	4.0- 30.0	70	31	44.3	15.0	2.0-200.0	87	36	41.4	15.0	2.0-200.0
Shiners	39	29	74.4	8.0	1.0- 55.0	28	10	35.7	5.0	1.0- 15.0	67	39	58.2	7.0	1.0- 55.0
Fireballs	296	220	74.3	8.0	5.0-140.0	94	68	72.3	12.0	0.3- 65.0	390	288	73.9	9.0	0.3-140.0
Total	1,590	937	58.9			1,265	624	49.3			2,855	1,561	54.1		

FIGURE 1.—Area of the eastern north Pacific bluefin tuna fishery.

waters occurs (except for a narrow band of very cold, rich upwelled water near shore south to San Juanico). Red crabs (*Pleuroncodes planipes*) are abundant in this area. Winds and weather are generally favorable for purse-seine operations after mid-June, but in April and May strong northwest winds severely restrict fishing.

From Punta Eugenia to Point Conception, the southern California offshore area typically exhibits the warm Catalina Gyre in association with cold, upwelled water centered off Ensenada and to the north of Point Conception. Hydrographic conditions in this region favor good filter feeding for bait fishes, and winds and weather improve in late July through September. Seldom is this district too warm for bluefin.

The occurrence of the various school types in the northern and southern areas of the fishery is nonrandom (chi square 985.20, $P<0.001$). Perhaps the most striking difference is the almost complete lack of jumping and boiling schools in the southern area and the predominance of breezers in this same area (Table 3). These differences may reflect differences in the feeding behavior of *T. thynnus* on different prey

species. McHugh (1952) and Alverson (1963) found differences in the stomach contents of albacore, yellowfin, and skipjack tuna in different geographical areas. McHugh noted that red crabs were the dominant food item for albacore off the Baja California coast, while anchovies and other baitfish dominated in fish stomachs taken from southern California waters. Blunt (1958) noted that of 168 *T. thynnus* taken off California in 1957, 70% had been feeding on anchovies. Longhurst (1967) observed that during normal years the distribution of *P. planipes* reaches from the area of Cedros Island south, while the range extends farther north during warm water years. This distributional pattern includes the entire area from which jumpers and boilers were almost entirely absent. While baitfish, like anchovies, are found in the southern area, previously cited studies indicate that red crabs may be the preferred food item. Since *P. planipes* is a relatively weak swimmer and occurs in very dense concentrations off southern Baja California, a modified filter feeding such as Sette (1950) described for Atlantic mackerel (*Scomber scombrus*) might be employed by *T. thynnus* while feeding on red crabs. On the other hand, the vigorous pursuit by scombroids feeding on forage fish is well known (Magnuson, 1963; Whitney, 1969).

The lack of jumping and boiling schools in the southern area also may be due to differences in the behavior of *T. thynnus* feeding on *P. planipes* and baitfish and a preference for the former when available. Comparisons of stomach contents of *T. thynnus* from the three school types would provide the necessary test of this hypothesis, but such information is not available. However, analyses of stomach contents for yellowfin from an area in which *P. planipes* was the dominant food item and from a second area in which fish were the dominant item have been made (Alverson, 1963). Yellowfin sets, which were from these same two areas (but at different times in 1965) and which were identified as to school type, showed significant differences (chi square 17.27, $P<0.01$) in the occurrence of jumping, boiling, and breezing schools (Table 4). Greater numbers of jumping and boiling schools and reduced numbers of breezers occurred in the area in which fish were the dominant food item, whereas the opposite was true in the area where red crabs were the dominant item. This lends support to our hypothesis that these school types reflect behavioral differences in the feeding patterns of *T. thynnus* and other tunas on red crabs and baitfish.

TABLE 4.—Comparison of breezing, jumping, and boiling yellowfin schools from the Gulf of Guayaquil and Baja California.[1]

Area	Breezers		Boilers		Jumpers	
	Number	Percent	Number	Percent	Number	Percent
Baja California[2]	183	91.5	1	0.5	16	8.0
Gulf of Guayaquil[3]	121	77.1	11	7.0	25	15.9
Total	304		12		41	

[1] Schooling data are for 1965 (Inter-American Tropical Tuna Commission, unpublished data).
[2] Stomach contents: fish, 19.4%; red crabs, 78.1% (Alverson, 1963)
[3] Stomach contents: fish, 76.9%; red crabs, 0.0% (Alverson, 1963) red crabs do not occur in the Gulf of Guayaquil.

If, in fact, many of the breezing schools in the southern area of the fishery are feeding upon red crabs, one would expect to find a greater percentage of successful sets on breezing schools in this area when compared with breezing schools taken in the northern area of the fishery. However the observed differences are not significant (chi square 2.18, $P>0.20$). It might be that if feeding breezers and nonfeeding breezers were compared that differences in percentage success between the two areas would be found.

The greater number of fireball schools observed in the northern area of the fishery may reflect a difference in the distribution of bioluminescent organisms. However, persistent stratus overcast in the southern California offshore zone during summer results from upwelled water coursing southward from Point Conception. As a result of this stratus overcast, the fishermen's ability to see fireballs at night may be significantly enhanced by eliminating background illumination from the moon and stars. The phenomenon requires further study.

VULNERABILITY TO CAPTURE

There were significant differences in vulnerability to capture, as indicated by percentage of successful sets (Table 2), among the five most common daytime schools (chi square 62.32,

$P<0.001$). These differences in vulnerability are most likely related to behavioral differences which affect a school's ability to avoid capture. Other factors such as water clarity, depth of thermocline, and water temperature also may be important. Two of the three most vulnerable school types were jumpers and boilers, both of which can be described as violently active schools in which individual fish are often in pursuit of baitfish. Shiner schools were also highly vulnerable to capture, yielding success rates of over 58%. It may be that shiners are subsurface feeding schools in which the "shines" are reflections of the operculum or of the lateral or ventral surfaces of the fish as they twist and turn in pursuit of their prey (Scott, 1969).

Three factors may be responsible for the greater vulnerability of these "feeding" schools: 1) feeding schools lack the organization of nonfeeding schools; 2) individual fish in feeding schools are less aware of threatening stimuli than are nonfeeding fish, and 3) feeding schools are more likely to remain in a localized area. The first two factors would increase a school's vulnerability to capture by delaying the time at which the fish are aware of potential danger and also by increasing the elapsed time before the fish react as a unit to this danger. The third factor would make it easier for the fisherman to anticipate the position of the school when he sets upon it. Another factor which should be mentioned is that a greater percentage of actively feeding schools may be located in areas of upwelling where cold, nutrient-laden waters generally result in decreased visibility. The effect of water clarity on percentage success has been discussed by Hester and Taylor (1965).

Breezing schools are generally schools moving in a single direction, often making sudden changes in depth, which makes it difficult for fishermen to anticipate the position of the school relative to the boat before setting. Greater cohesiveness is apparent among breezing schools, and it appears that there is a greater awareness of potential danger than in feeding schools.

Blackspots are subsurface schools which are difficult to locate and to catch. The very nature of this school type suggests that a greater number of them might be expected to be found in areas with a deep thermocline and clear surface waters. Green (1967) has shown that schools encountered in areas with a deep thermocline are less vulnerable to capture than are schools found in areas with a shallow thermocline. In addition, the deeper a school is in the water column, the closer it is to one possible route of escape: the bottom of the net. All of these factors would contribute to the greater rate of escapement observed for black spots.

We have omitted from this section any consideration of fireball schools. The reasons for the greater vulnerability of nighttime schools (discussed in a later section) are equally applicable to fireballs.

CATCH PER SUCCESSFUL SET

There were significant differences in the mean size of the six most common schools (Figure 2). Black spots and breezers were the two largest school types. The three feeding school types, jumpers, boilers, and shiners, were the smallest. The disruption of schooling behavior during feeding activity (Magnuson, 1963; Whitney,

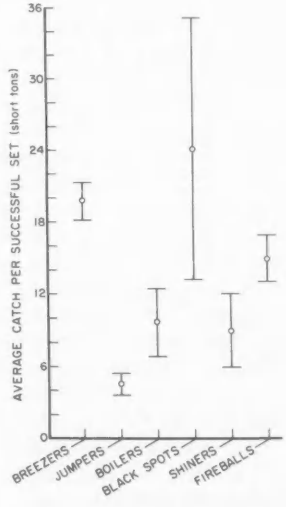

FIGURE 2.—Average catch (short tons) of each of the six most common bluefin tuna school types.

1969) may account, in part, for the reduced size of these schools. However, the observed disruptions have occurred within a relatively small area and were in response to an immediately available food source. It seems unlikely that the area involved would exceed that area normally encircled by a purse seine. We believe that the reduced size of the actively feeding daytime schools is the result of the relatively larger nighttime schools separating into smaller foraging schools with the rapid onset of higher light intensities at dawn.

Various mathematical treatments have shown the advantages of schooling to predator and prey alike (Brock and Riffenburgh, 1960; Olson, 1964). Olson contends that the swept path of an individual predator, and hence its chances of encountering a prey species, would be greatly increased if it traveled in a school rather than singly. In addition, we suggest that there is an optimum school size (number of individuals within the school) for feeding. Beyond this size, there may be increasing duplication of individual visual fields, making it more efficient for the fish to break down into a number of smaller schools in order to increase the area covered and thereby increase their chances of encountering and capturing prey. It may be also that individuals in schools beyond a certain size obtain less energy than those foraging in smaller schools. This school size would be dictated by a number of factors, such as visual acuity of the predator, type of prey, and prey density. A patchy distribution of a relatively fast moving schooling prey (e.g., anchovies) and a relatively uniform distribution of a slow moving prey (e.g., red crabs) within a localized area require different hunting and feeding strategies. Other factors may also be important (see Shaw, 1962; Breder, 1967).

TIME OF DAY

Fishermen recorded time of day for a total of 4,925 sets. Of these, 4,144 were made without aircraft assistance. The number of sets varied with time of day (Figure 3), as did the catch per successful set (Figure 4), percentage of successful sets (Figure 5), and occurrence of the various school types (Figure 6).

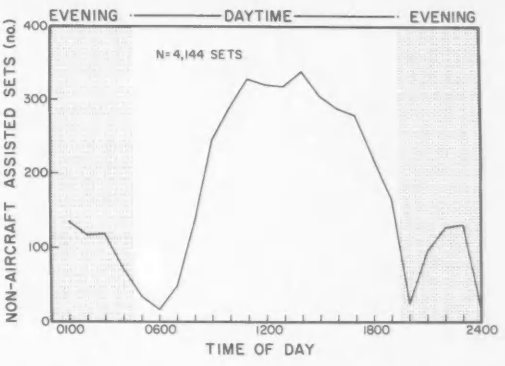

FIGURE 3.—Variation of the number of purse-seine sets on bluefin tuna in relation to time of day.

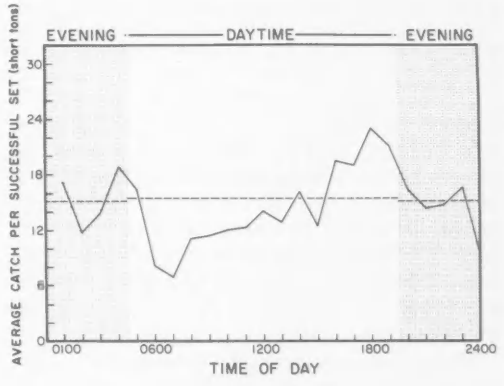

FIGURE 4.—Average catch per successful purse-seine set (short tons) on bluefin tuna in relation to time of day. (Not assisted by aircraft. Grand average catch for daylight and evening hours is indicated by the dashed lines.)

The percentage of successful sets on bluefin schools was significantly greater during the evening hours than it was during the day (chi square 126.56, $P<0.001$).

Whitney (1969) suggested that the greater vulnerability of tuna to capture at night was due to decreased visibility of the net and decreased activity of the fish. Recent laboratory work using *Engraulis mordax* has shown a diel rhythm

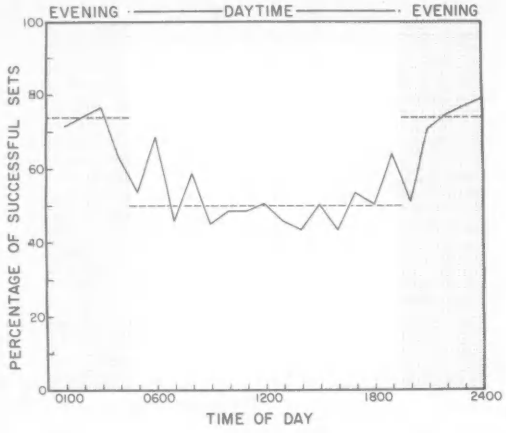

FIGURE 5.—Variation of percentage success of purse-seine sets on bluefin tuna in relation to time of day. (The grand average percentage success for daylight and evening hours is indicated by the dashed lines.)

in their direction of escape from a net cylinder (Scott, 1970). The tendency of *E. mordax* to use the bottom escape route during the day and to be random in their direction of escape at night would increase their vulnerability to capture at night by bottom-closing nets. If this same pattern is found in *T. thynnus* and other tunas, it would help to explain the observed differences in percentage success.

There were significant differences also in percentage success during the daylight hours (chi square 37.12, $P<0.01$). This is in contrast to the lack of significant variation in percentage success during the day reported by Whitney (1969).

The distribution in time of the five most common daytime school types is nonrandom (chi square 259.15, $P<0.001$). The three actively feeding schools were most common from 0700 to 1100 (Figure 6). During this period, these school types account for more than 42.2% of the identified school types.

The greater number of feeding schools in the early morning hours reflected in an increased percentage success during the early morning hours (0500-0800) when all school types are combined (Figure 5). The decrease in percentage success at 0700 is accounted for by a decrease in the percentage success of nonfeeding schools rather than a decrease in the number of feeding schools or a decrease in the vulnerability of feeding schools to capture. While the number of feeding schools increases until 1100, this is not reflected in an increase in the overall percentage success because of an accompanying increase in the number of nonfeeding schools (Figure 6). There appears to be a slight increase in the percentage of feeding schools during the late afternoon hours (1600-1900) (Figure 6B,C,D) which suggests that there may be two peaks in feeding

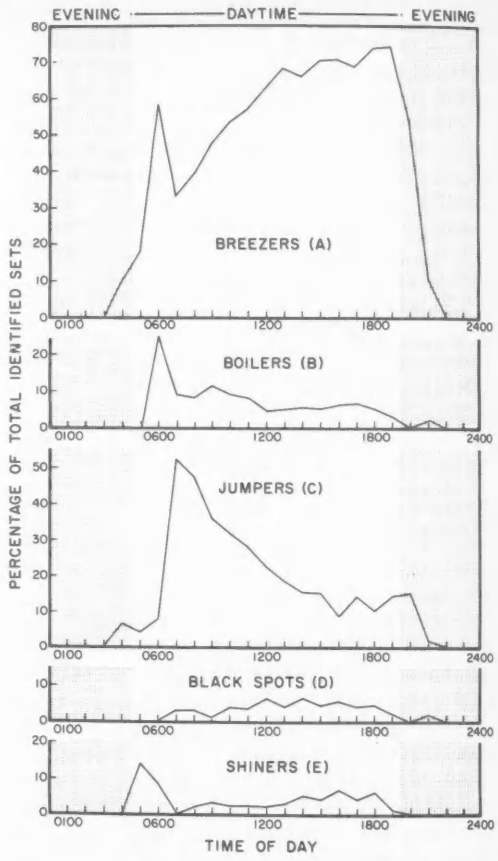

FIGURE 6.—Variation of occurrence of the five most common bluefin tuna school types in relation to time of day.

activity for *T. thynnus*, as has been shown for albacore (Iversen, 1962), bonito (Suyehiro, 1938), and yellowfin tuna (Uda, 1940; Waldron and King, 1963). However, the late afternoon increase in feeding activity is a minor one.

The percentage success does not vary significantly with respect to time of day in the four most common school types: breezers, jumpers, boilers, and fireballs (Figure 7). However, there is an increase in percentage success during the late afternoon hours for the three daytime schools, suggesting that the observed increase in percentage success during the late afternoon hours is due to the environmental factors cited by Whitney (1969). Additional data are needed for the late afternoon hours in order to further clarify this question.

The differences in school size between daytime (14.8 tons) and nighttime sets (14.4 tons) were not significant. However, there were differences noted in distribution of sets by 5-ton intervals (chi square 18.80, $P<0.05$) with fewer small schools (5 tons or less) being taken at night. The reduced percentage of small schools could be the result of a greater number of these schools being passed up by the fishermen at night, possibly because of reduced visibility to the mastman. We have no evidence to suggest a real decrease in the number of small schools during night hours as opposed to daytime.

There was a marked variation in average school size within the daylight hours; the size of schools steadily increased from 6.9 tons at 0700 to 22.5 tons at 1800 hours (Figure 5). This pattern is not apparent in the jumping and boiling schools, however (Figure 8).

The early morning decrease in school size initially may be a response to increased light and feeding activity as suggested by Whitney (1969); subsequently the relatively large nighttime schools break down into several smaller foraging schools and begin their search for food. The time elapsed between the reduction in school size and subsequent occurrence of large numbers of feeding schools might thus be the time required to encounter prey and begin to feed. We believe that the reduction in the number of feeding schools after 1100 hours reflects an increasing number of fish whose hunger is sated.

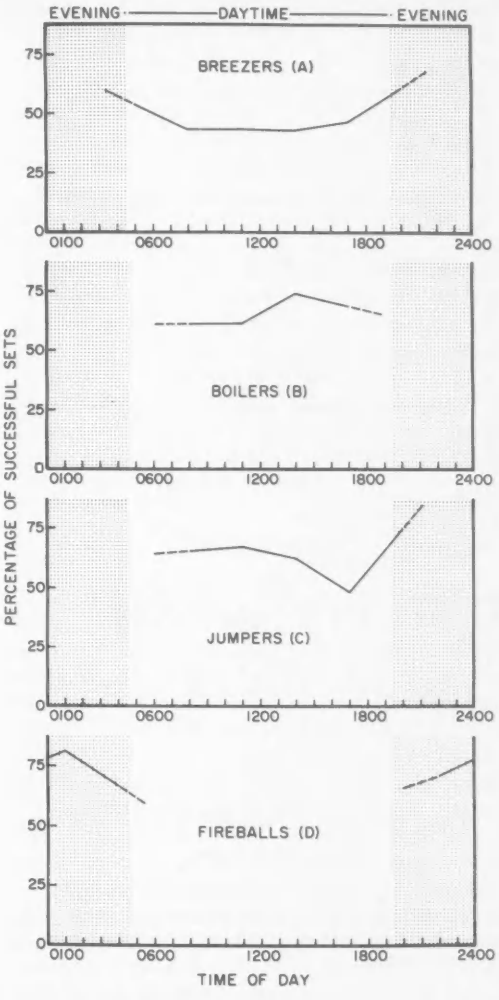

FIGURE 7.—Variations of percentage success on the four most common bluefin tuna school types in relation to time of day.

The gradual increase in school size during the daylight hours may be due to regrouping of the smaller schools through random encounters as suggested by Whitney (1969). The reduction in school size in the late afternoon cannot be accounted for by an increase in the number of

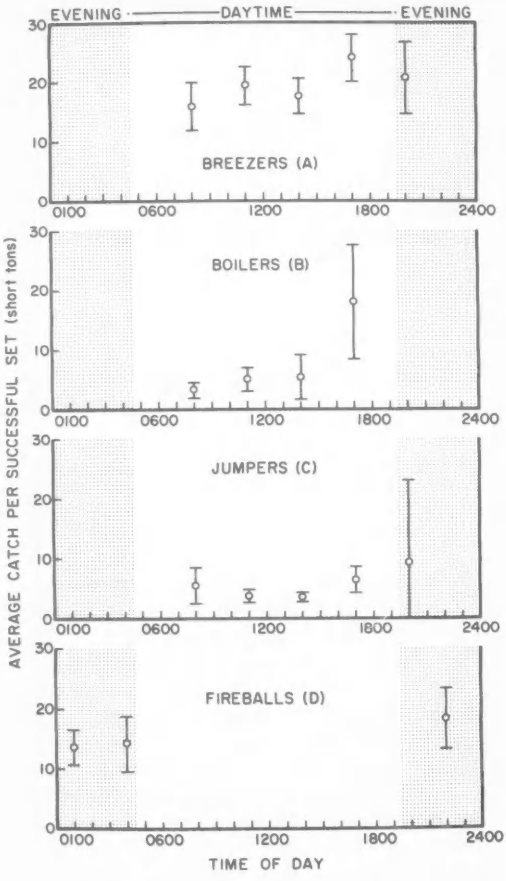

FIGURE 8.—Variation in the average catch per successful set on the four most common bluefin tuna school types in relation to time of day. (Catch in short tons grouped by 3-hr intervals.)

feeding schools and is most likely due to a reduction in available light (Whitney, 1969).

The lack of significant variation in either percentage success or catch per successful set within a single school type suggests that the observed variations in these two factors when all school types are considered together is due more to differences in the occurrence of the various school types within the daylight hours than it is to environmental factors such as daylight. However, the increased vulnerability of breezing and jumping schools during the late afternoon hours may be due to reduced light intensity during that period. Unfortunately it is the early morning and late afternoon hours for which we have the fewest data.

EFFECT OF AIRCRAFT ASSISTANCE

Aircraft assistance on bluefin tuna sets gave a significantly greater percentage of success than unassisted sets (chi square 8.69, $P<0.01$). The average catch in assisted sets also was consistently larger than in unassisted sets (Table 5). These differences have also been shown for yellowfin and skipjack tuna. The reasons for the greater size and vulnerability of schools set upon with aircraft assistance have been discussed elsewhere (Schaefer, 1962). In addition, however, the greater average size of assisted sets may be due to the disproportionately fewer small schools (jumpers and boilers) and a greater number of large schools (black spots and shiners) captured with aircraft assistance.

The two most visible schools, jumpers and boilers, have the smallest percentage of assisted sets (Table 6). The greater height of the air-

TABLE 5.—Effect of aircraft assistance on purse-seine sets for bluefin tuna, 1960-67.

Year	Percentage of sets assisted by aircraft	Percentage success		Catch per successful set (short tons)	
		Assisted	Unassisted	Assisted	Unassisted
1960	2.5	75.0	47.3	65.7	29.3
1961	14.5	79.0	63.8	17.7	12.6
1962	12.6	72.2	65.7	17.1	9.8
1963	20.4	45.8	41.2	20.5	21.2
1964	12.1	62.8	59.5	13.3	9.3
1965	20.2	43.4	48.0	19.3	14.7
1966	13.9	60.5	46.6	22.5	15.9
1967	11.5	51.5	43.1	23.6	19.5
Average	15.3	54.9	53.0	19.3	14.2

TABLE 6.—Comparison of effectiveness of aircraft assistance by school type for purse-seine sets on bluefin tuna, 1960-67.

School type	Number of sets	Aircraft assisted sets	
		Number	Percent
Boilers	221	17	7.7
Jumpers	639	44	6.9
Breezers	1,871	359	19.2
Shiners	111	44	39.6
Black spots	137	50	36.5
Totals	2,979	514	17.3

TABLE 7.—Comparison of average catch per successful set and percentage success for assisted and unassisted sets on the four most common daytime bluefin tuna school types.

School type	Average catch per successful set (short tons)		Percentage success	
	Assisted	Unassisted	Assisted	Unassisted
Jumpers	29.1	4.7	87.5	63.7
Breezers	21.3	19.8	47.9	46.2
Shiners	15.2	9.0	63.6	58.2
Black spots	23.0	25.0	50.0	41.4

craft and, therefore, the greater area and depth of visibility to an airborne spotter would increase the possibility of spotting the subsurface schools which otherwise might not be visible to observers aboard a vessel (Green, 1966).

However, there are differences in both catch per successful set and percentage success between assisted and unassisted sets in the same school type (Table 7). All of the schools show increased percentage success with aircraft assistance, and all but black spots exhibit larger school size with aircraft assistance. This indicates that the larger size and greater vulnerability of schools set on with aircraft assistance is the result not only of the unequal distribution of the various school types between assisted and unassisted sets but also due to the skill of the airborne spotter in locating larger schools, and by his ability to increase the ship's chances of capturing the school.

MULTIPLE SCHOOLING CHARACTERISTICS

Almost every possible combination of the 13 different school types occurred. However, schools recorded as showing two or more behavioral types made up a very small percentage of the total sets made. Whether this is indicative of the actual occurrence of these types or the propensity of the fishermen to record them and the log abstractor to copy them is unknown. The problem of multiple schooling types has been discussed elsewhere (Scott, 1969).

Bluefin were captured in sets with yellowfin, skipjack, and albacore. Bluefin were also observed schooling with whales (Table 1). In spite of large amounts of flotsam and jetsam occurring in the fishing area, only two reports of this school type were logged. No porpoise-associated schools were reported. This is probably due to the absence of porpoise in the areas in which bluefin are generally found. Further data are needed before meaningful conclusions can be drawn with respect to the occurrence or lack of porpoise-associated schools in the bluefin fishery.

DISCUSSION

Striking differences in catchability, size, and geographical distribution have been demonstrated for the various types of bluefin schools. Suggestions as to possible reasons for these differences are offered but in most instances additional behavioral information is needed. We hope that definitive field and laboratory behavioral studies will be made in order to further strengthen or disprove interpretations which we have drawn from the logbook data. Studies on other scombroids would also be valuable for comparative purposes. The possibility that there are two or more types of breezing schools should be studied in detail, and the percentage success of sets on breezing schools known to be feeding compared with nonfeeding schools should also be investigated.

ACKNOWLEDGMENTS

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and counsel. Dr. Richard R. Whitney originally suggested this study to us, and Dr. John R. Hunter gave valuable advice during the study. Roger E. Green assisted in constructing the original ADP format for data analysis. Dr. Richard Whitney, Dr. John R. Hunter, and Craig J. Orange reviewed the manuscript.

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NUTRIENT INVERSIONS IN THE SOUTHEASTERN TROPICAL PACIFIC OCEAN [1, 2]

WILLIAM H. THOMAS[3]

ABSTRACT

Nutrient inversions in the offshore southeastern tropical Pacific Ocean are described. At a typical station nutrients such as nitrate and phosphate are high at the surface, are at a minimum at about 100 m depth, and then increase at greater depths. Silicate follows this distribution to a lesser degree. These inversions occur from lat 8 to 15°S and are more pronounced in sections along long 126°W and 119°W than in sections farther east. The nutrient minimum is associated with water having a salinity maximum. It is suggested that such water may have acquired its characteristics in the mixed layer in areas to the south or southeast where the nutrients were depleted by phytoplankton, and has then sunk below high-nutrient and relatively fresh water carried westward from the Peru Current. However, the nutrients may also have been depleted in situ since the low-nutrient water contains a maximum amount of chlorophyll.

In water where nutrients are limiting phytoplankton growth, they are typically at minimum concentrations in the surface and mixed layer, increase at the thermocline, and reach a maximum below this depth. Such typical distributions are shown by Sverdrup, Johnson, and Fleming (1942) and by Riley and Skirrow (1965). The EASTROPAC data show such distributions in all parts of the nutrient-poor water of the northeastern tropical Pacific Ocean (Thomas, 1970, 1971, and unpublished data).

The purpose of this paper is to describe a different distribution occurring in the south tropical Pacific Ocean in which nutrient concentrations are typically high at the surface, are at a minimum at depths just above the permanent thermocline, and then increase at greater depths. In this paper this unusual distribution is called a "nutrient inversion."

METHODS

The EASTROPAC sampling program and vessel track charts are given in the Introduction to the EASTROPAC Atlas (Love, 1970). Nutrients (nitrate, nitrite, phosphate, and silicate) from Nansen bottle samples were analyzed with the Technicon® Autoanalyzer[4] using the methods of Armstrong, Stearns, and Strickland (1967) or manually, using methods outlined by Strickland and Parsons (1968). Vertical sections along given longitudes were plotted by computer (Love, 1970).

RESULTS

During February-March 1967, nutrient inversions were found at several stations near lat 10°S and along long 112°W, 119°W, and 126°W. A typical inversion is shown in Figure 1 for EASTROPAC Station 11.140; three nutrients—nitrate, phosphate, and silicate—show minima at

[1] Contribution from the Scripps Institution of Oceanography.

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[4] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

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about 60 to 140 m depth. The inversion is particularly pronounced for nitrate, where concentrations in the minimum reach nearly undetectable levels.

The inversions are also apparent in vertical sections. Section 11-NO_3-V2 from the EASTROPAC Atlas (Thomas, 1971) is shown in Figure 2. This section was taken along long 119°W in February 1967 and shows that the inversion extends from about lat 8° to 15°S.

Similar sections occupied in February-March 1967 showed the inversions along long 126°W (from lat 8° to 15°S) and along long 112°W (from lat 8° to 10°S). The nitrate data show inversions much more clearly than phosphate or silicate data. Inversions in nitrate concentration are barely detectable in sections to the east at these latitudes—along long 105°W, 98°W, or 92°W—because concentrations at similar depths are higher. The inversion phenomenon is most pronounced in the westerly sections of the EASTROPAC data.

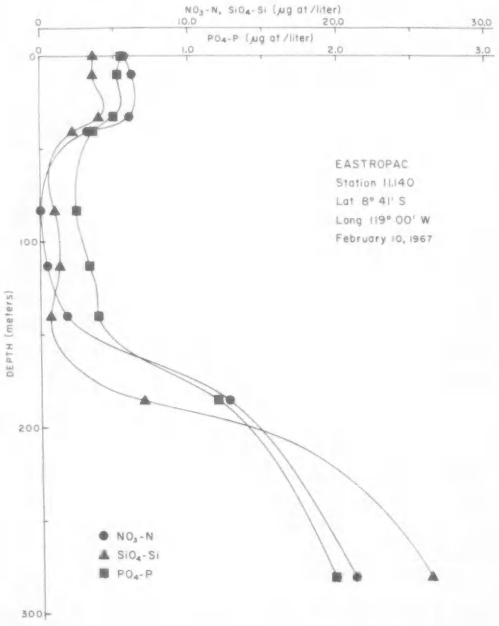

FIGURE 1.—Distribution of nitrate-N, silicate-Si, and phosphate-P concentrations with depth at EASTROPAC station 11.140, February 10, 1967.

The nitrate inversion was again detected in the southern summer of 1968 (February-March) during the third EASTROPAC survey (Thomas, unpublished Atlas data). At that time it was apparent along long 119°W (from lat 9° to 15°S), but not at more easterly longitudes. The long 126°W line was not sampled at this time.

It is not known whether inversions along these longitudes are permanent, nonseasonal features, since the second EASTROPAC survey during the southern winter (August-September 1967) and the EASTROPAC monitoring cruises (which took place between the multiship surveys) reached only lat 5°S. At this latitude inversions were not found.

DISCUSSION

Such nutrient inversions were not commented upon prior to EASTROPAC because this was the first expedition to measure a relatively complete suite of nutrients over a broad area of the eastern tropical Pacific Ocean. However, there are indications of such inversions in phosphate at many of the EQUAPAC stations taken in August-September 1956 during Cruise 35 of the RV *Hugh M. Smith* (Austin, 1957). The *Smith* traversed long 135°W, 143°W, 151°W, and 160°W from about lat 3°N to 19°S, and many of the stations taken from lat 5°S to 19°S show minimum phosphate values at about 100 to 160 m depth. The inversions probably would have been readily apparent if nitrate analyses had been made during *Smith* Cruise 35.

Such inversions are not found in stations taken from lat 7° to 15°S and long 162°W and 175°W in the nitrate, phosphate, or silicate data from cruise STYX in June-July 1968 (Reid, unpublished data). However, they are found to a slight extent in this same area when the nitrate data from a *Gascoyne* cruise in 1961 are examined (C.S.I.R.O., 1967).

This water having a minimum nutrient concentration has a high salinity. Figure 3 (from Tsuchiya, unpublished Atlas data) shows a salinity section along long 119°W in February 1967 from the EASTROPAC observations. The maximum in salinity clearly corresponds to the nutrient minimum shown in Figure 2.

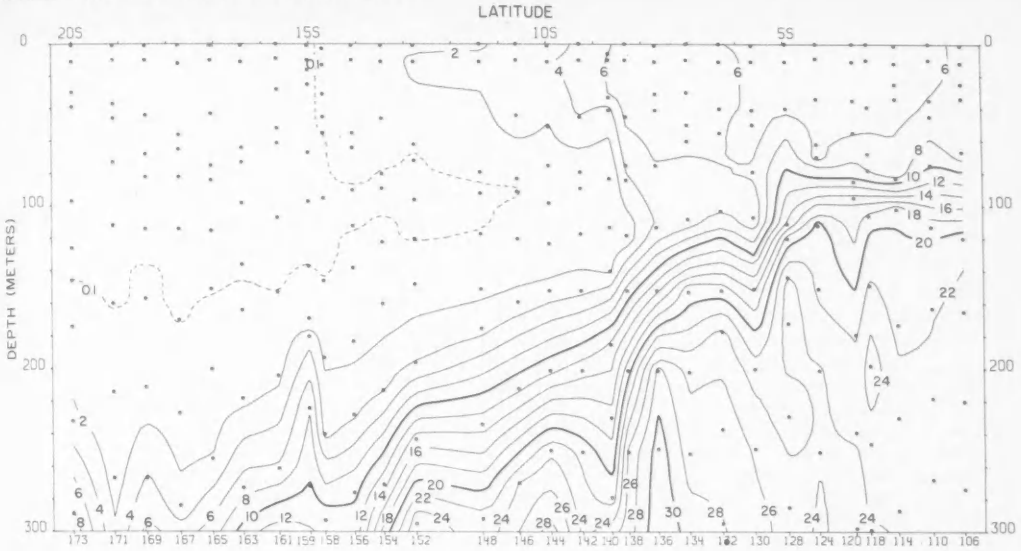

FIGURE 2.—Vertical distribution of nitrate-N (μg-at/liter) along long 119°W from lat 1°14′S to 20°00′S, February 7-14, 1967.

It is not easy to explain these distributions. There is a possibility that the subsurface water has been depleted of nutrients in situ since this water has a maximum chlorophyll concentration (Owen and Zeitzschel, 1971). On the other hand, one can envisage two water masses that impinge on each other. One of these, the low-salinity, high-nutrient, surface, and near-surface water, may have drifted to the west from the Peru Current via the South Equatorial Current. The horizontal maps of nutrients at 10 m (Thomas, 1971, and unpublished Atlas data) show that near-surface nutrients are high at these latitudes from Peru at least west to long 126°W, and Wyrtki (1966, Figures 1 and 2) indicates such westward surface currents. One can then envisage that the second water mass, containing high-salinity water that is depleted in nutrients, has its origin in the South Pacific Gyre and has sunk below the first water mass and drifted in from the southeast. Geostrophic flow of the maximum salinity water is predominantly from the east or southeast in the EASTROPAC area (Tsuchiya, unpublished Atlas observations) and similar flow from the east was shown by Tsuchiya (1968) in his Figure 6 for the 300 cl/t δ_t surface which has a depth of 50-100 m in this area. It should be mentioned that the data are very sparse in the area to the south and southeast of these inversions and their full explanation may await further data collection and analysis.

The nitrate data show the inversion more clearly than data for other nutrients, because nitrogen is more limiting to phytoplankton than phosphate or silicate in near-surface water to the south of these inversions (Thomas, 1969) and is possibly limiting in the water where the nutrients were depleted.

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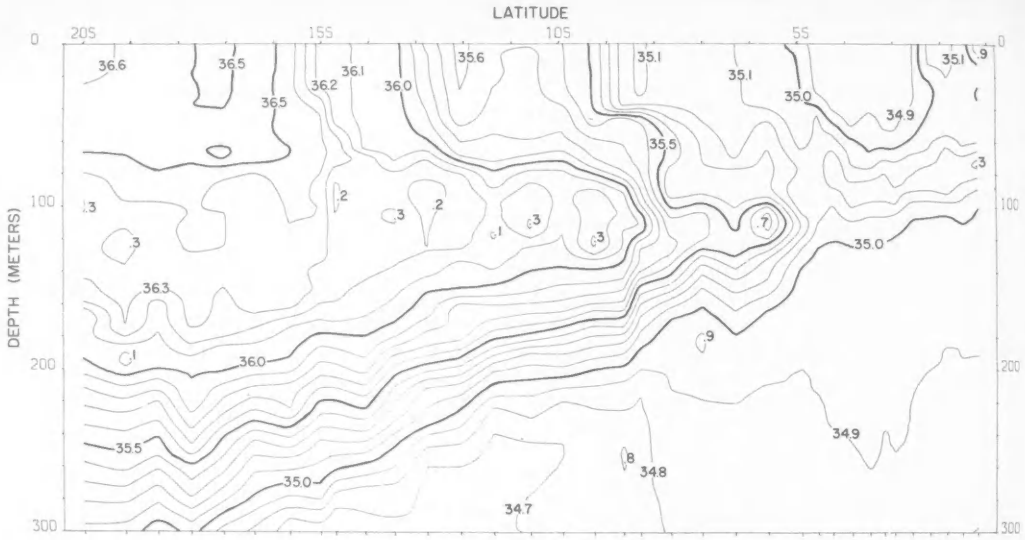

FIGURE 3.—Vertical distribution of salinity (‰) along long 119°W from lat 1°14'S to 20°00'S, February 7-14, 1967.

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GROWTH HORMONE- AND PROLACTIN-LIKE PROTEINS OF THE BLUE SHARK (*PRIONACE GLAUCA*)

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ABSTRACT

The two major disc-electrophoretic components, designated as "slow" and "fast," which are seen in fresh homogenates of the pars distalis of the blue shark (*Prionace glauca*) pituitary gland were isolated. Some alteration of the proteins occurred during the purification as evidenced by appearance of a slightly faster migrating band in each. The slow component and its altered form had a molecular weight of 22,000 daltons; the fast, and its modified form, 20,000 daltons. The two proteins were very similar chemically and immunologically, but definite differences were noted. Both gave a precipitin line with antiserum to mouse growth hormone, although quantitatively different, but neither reacted to antiserum to mouse prolactin. The peptide maps of the two proteins were identical except for three peptides. Both contained two moles of tryptophan and six half-cystine residues. These results indicate that the pars distalis of the blue shark contains two very similar proteins that resemble both growth hormone and prolactin of mammals.

There have been few reports that have dealt with the isolation of purified preparations of growth hormone and prolactin from pituitary glands of fish. This most probably stems from the fact that there is no convenient bioassay for these piscine hormones. Wilhelmi (1955) purified growth hormone from the hake; Donaldson, Yamazaki, and Clarke (1968) reported on prolactin of salmon; and Emmart and Bates (1968) described purification of prolactin of the pollack. As a means of circumventing bioassays, we thought that disc electrophoresis might prove successful. The method has been used by us to follow the purification of growth hormone and prolactin of the mouse (Cheever, Seavey, and Lewis, 1969), human (Lewis, Singh, and Seavey, 1971), and turtle (Singh, Seavey, and Lewis, 1972).[4] The approach appeared even more reasonable for the isolation of the shark hormones when we found that the electrophoretic pattern of the pars distalis extract contained only two major bands. This has been found to be the case for many species, and growth hormone usually has been identified as the slower migrating of the two bands (Nagy, Kurz, and Baranyai, 1969; Nicoll and Nichols, 1971; Nicoll and Licht, 1971). An exception to this has been found in the human (Friesen, Guyda, and Hardy, 1970; Lewis et al., 1971) where growth hormone is more acidic than prolactin and, therefore, migrates more rapidly during electrophoresis at an alkaline pH.

Making the assumption, then, that the two major bands seen in the electrophoretic pattern of the shark pituitary extract were growth hormone and prolactin, we devised a procedure for their isolation and used electrophoresis as a means of following the purification. The isolation procedure and some properties of the purified proteins are described in this communication.

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MATERIALS AND METHODS

DISC ELECTROPHORESIS

Our use of the method has been described (Lewis, Litteria, and Cheever, 1969). For routine analytical analyses the gel was made of 7.5% acrylamide and 0.25% N-N'-methylenebisacrylamide. For quantitation of the amount of protein in a stained band, ethylene diacrylate was substituted for the cross linking agent.

MOLECULAR WEIGHT

Molecular weights were estimated by using disc electrophoresis (Cheever and Lewis, 1969).

PEPTIDE MAPPING AND AMINO ACID ANALYSES

Our procedure for peptide mapping has been described (Seavey and Lewis, 1971). Total amino acid analyses were done on performic acid oxidized samples by means of automated analysis. Tryptophan was determined by the method of Beaven and Holiday (1952).

IMMUNODIFFUSION

Mouse growth hormone prepared by the method of Cheever et al. (1969) was used for immunization of monkeys; antiserum to mouse prolactin was produced in rabbits by using hormone prepared as described in the same publication. The antiserum to mouse growth hormone was not contaminated with antibodies to mouse serum proteins or mouse prolactin; the antiserum to mouse prolactin, likewise, did not give a precipitin line with serum proteins nor did it cross react with mouse growth hormone. Immunodiffusion was carried out by the method of Ouchterlony.

COLLECTION AND STORAGE OF GLANDS

The pars distalis was removed within 30 min after the animals were killed and immediately homogenized in water (5 ml/g wet tissue) at 5°C. The homogenate was stored at —20°C until it could be fractionated. This procedure was used to minimize alteration of the proteins, as judged by electrophoretic analysis. More rapid changes occurred when the glands were stored intact.

ISOLATION PROCEDURE

All processes were carried out at 5°C. The pars distalis (7.6 g wet weight) from 87 blue sharks were homogenized in 38 ml water. The pH of the homogenate was adjusted to 10 with dilute NaOH and made 10^{-3} M in diisopropylphosphofluoridate. After 4 hr of stirring the homogenate was centrifuged at 20,000 × g for 40 min. The supernatant fluid was decanted, its pH lowered to 8 with dilute HCl and set aside. The insoluble residue was suspended in 0.05 M Na_2CO_3-$NaHCO_3$ buffer, pH 10 (2.5 ml/g original tissue) and stirred for 16 hr. After centrifugation, the supernatant fluid was pooled with the first extract and the pH of the mixture adjusted to 8. The insoluble tissue was discarded when electrophoresis showed that all the desired components had been extracted.

The crude extract was concentrated to about 15 ml on a Diaflo UM-10 membrane[5] (Amicon, Lexington, Mass.) and placed on a column of Sephadex G-150, 5 × 90 cm and developed with 0.01 M NH_4HCO_3. Every fifth tube was analyzed by disc electrophoresis (100 μliter aliquots) and the tubes that contained the two proteins that were assumed to be growth hormone and prolactin were combined and concentrated to about 10 ml on a UM-10 Diaflo membrane. Figure 1 shows the elution pattern of the Sephadex column; the stippled area contained the desired components, S and F.

The concentrated solution from the Sephadex chromatography was applied to a column of DEAE-cellulose (Whatman 32) with dimensions of 0.9 × 10 cm and which had been equilibrated with 0.01 M NH_4HCO_3. The flow rate was 38 ml/hr. Once the sample had been applied, the column was washed with 25 ml of 0.01 M NH_4HCO_3. No appreciable amount of protein

[5] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

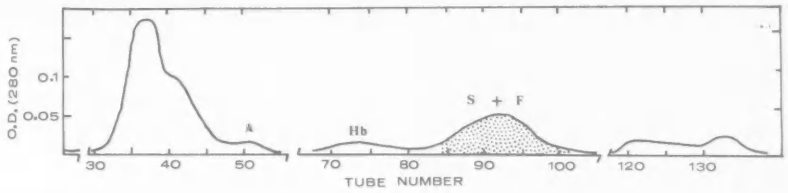

FIGURE 1.—Elution pattern obtained by chromatography of an alkaline extract of the pars distalis on Sephadex G-150. Each tube had a volume of 14 ml. The slow and fast electrophoretic components (S and F) were found in the stippled area. A = albumin; Hb = hemoglobin.

was eluted by the process. A gradient was next begun and was made by mixing equal portions (100 ml each) of 0.01 M and 0.1 M NH_4HCO_3. This eluted a major peak. A second gradient of equal volumes (150 ml each) of 0.1 M and 0.2 M NH_4HCO_3 was begun immediately. This gradient eluted a second peak. The results obtained with the DEAE-cellulose chromatography are shown in Figure 2.

The two major peaks eluted during chromatography on DEAE-cellulose were lyophilized. The yield of component F was 43 mg; that of component S, 22 mg.

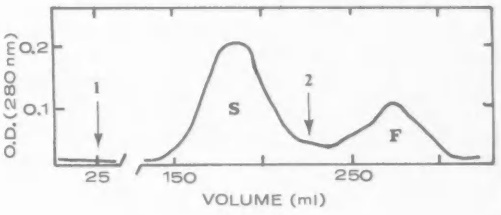

FIGURE 2.—Elution pattern obtained by chromatography of the S + F fraction of Figure 1 on DEAE-cellulose. The first gradient was begun at 1 and a second at 2. The S and F components were resolved as indicated in the drawing.

RESULTS

ELECTROPHORETIC ANALYSES

Pituitary Extracts

The water homogenate of the pars distalis showed two principal electrophoretic components when analyzed within 30 min after the sharks were taken from the sea. An alkaline extract of the glands, made about a week later, gave an almost identical pattern except that a definite band could be seen just ahead of each of the major components S and F. This is shown in Figure 3. The S and F components were assumed to be growth hormone and prolactin, respectively, and were the components for which we devised an isolation procedure. The bands designated as A, B, and C were minor components seen in both the water homogenate and the alkaline extract. A fast component also migrated near the buffer front.

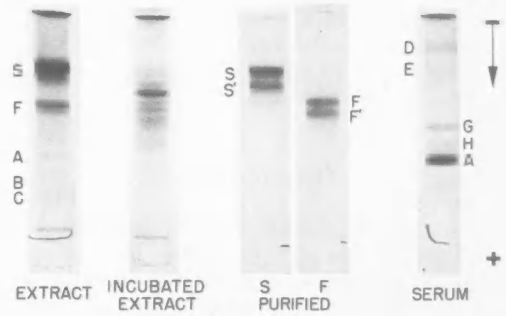

FIGURE 3.—Electrophoretic patterns (pH 9.5) of various shark materials. The pattern for the incubated sample was obtained after heating the alkaline extract at 37°C for 2 hr. S and F are the slow and fast components; S′ and F′ are the bands that formed during isolation of the proteins. Components A through E are discussed in the text. A thread marks the original buffer front (bromphenol blue) in two of the gels.

The conversion of the S and F bands to more rapidly migrating components became more pronounced as the fractionation of the extract progressed. As seen in Figure 3, by the time the proteins were isolated, each was a definite doublet. The new components are designated as S′ and F′. The same type of alteration of the S and F proteins occurred even during storage of intact glands at —20°C. After one month, the S′ and F′ were of about equal intensity to that of the original S and F bands. The alteration was barely noticeable however in a water homogenate of glands stored for the same length of time at —20°C. We determined also how incubation at 37°C affected the conversion of components S and F. After 2 hr at that temperature, S and F had virtually disappeared and a new band intermediate in mobility between S and F was present. This is shown in Figure 3. All bands disappeared if the extract was left at 37°C for 6 hr.

Serum

To determine whether either S or F might be serum components we analyzed a sample of shark serum (Figure 3). There was a faint band (E) in the region of S but none for F in gels of 7.5% acrylamide. At 10% and 12% acrylamide band E was more retarded than S, however. Component A of the pituitary extract lined up with the major component of serum in four concentrations of acrylamide.

PURIFICATION

The elution pattern obtained from chromatography of the alkaline extract on Sephadex G-150 is shown in Figure 1. As described in the experimental section above, the S and F components were located by disc electrophoresis and both were found in the same elution peak (stippled area). The peak of high molecular weight material at the beginning of the elution pattern gave an abnormally high optical density reading because of opalescence. The peak designated as A had the same electrophoretic properties of band A of Figure 3 and, as indicated above, was presumed to be albumin. The peak eluted just before S and F was labeled Hb (hemoglobin) because of its red color. Electrophoretically the material gave two very diffuse bands.

Figure 2 shows the elution pattern obtained by chromatography of Sephadex peak S + F on DEAE-cellulose. No protein was eluted with 0.01 M NH_4HCO_3. The first major peak, found to be F by electrophoretic analysis, was eluted by gradient 1 (0.01 M to 0.1 M NH_4HCO_3). A second gradient (0.1 M to 0.2 M NH_4HCO_3) eluted a second peak which was found to be component F by electrophoresis. The shoulder on the leading edge of peak F was probably a result of a small, rapid increase in ionic strength when the second gradient began.

The material of peaks S and F were lyophilized. The yield of S was 43 mg and 23 mg for F. Figure 3 shows the electrophoretic pattern of each of these samples. That each was a doublet was a result of alteration that took place during isolation. The conversion became progressively more pronounced during the purification.

MOLECULAR WEIGHTS

The molecular weights of components S and F as seen in electrophoretic patterns of the alkaline extract were S = 22,000 and F = 20,000. Identical values were obtained when the purified S and F fractions were analyzed. Likewise S′ and F′ had molecular weights indistinguishable from the corresponding S or F form although the molecular weight determination is accurate only to ± 2,000. The log R_m vs. gel concentration curves for these components are shown in Figure 4. Of significance was the fact that there was a greater charge difference between S and S′ than between F and F′. This is additional evidence that S and F are different substances. The slopes of the curves of Figure 4 were converted to molecular weight values by reference to a standard curve constructed from proteins of known molecular weight (Cheever and Lewis, 1969).

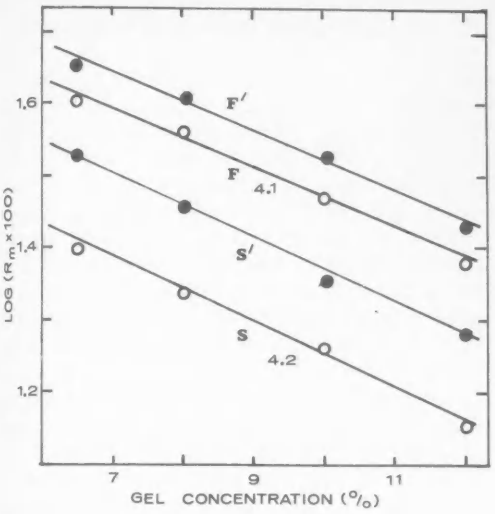

FIGURE 4.—A Ferguson plot of the relative mobility (R_m) of the S and F components and their altered forms (S′ and F′) versus the concentration of acrylamide used for the gel-electrophoresis.

The molecular weights of the other electrophoretic components seen in Figure 3 were A = 68,000; B = 65,000; C = 60,000; D = 47,000; E = 71,000; G = 64,000; H = 72,000.

IMMUNODIFFUSION

The purified preparations of S and F, which also contained S′ and F′, respectively, produced a precipitin line when tested against antiserum to mouse growth hormone (Figure 5). When tested at the same concentration, S gave a more pronounced line than did F. Neither preparation gave a precipitin line with antiserum to mouse prolactin.

AMINO ACID COMPOSITION

Table 1 gives the amino acid analyses of components S and F. The composition of the two proteins was quite similar but there were definite differences and component S had a greater total number of amino acids. Both contained six half-cystines and two tryptophans.

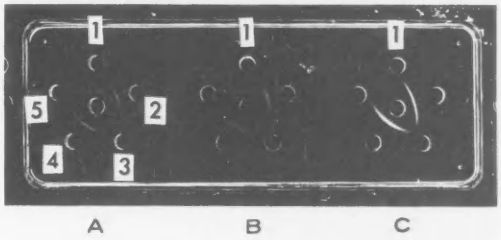

FIGURE 5.—Immunodiffusion plate for the S and F proteins. Antiserum to mouse growth hormone (10 μliter) was in the center well of A and B; antiserum to mouse prolactin was in the center well of C. The outer wells of A contained: **1**, 10 μg component S; **2** and **5**, 5 μg mouse growth hormone; **3**, 5 μg component S; **5**, 2 μg component F. The outer wells of C contained: **1**, 10 μg component S; **2**, 5 μg mouse prolactin; **3**, 10 μg component F; **4**, 5 μg mouse prolactin. The picture was taken after 24 hr at room temperature.

TABLE 1.—Amino acid composition of performic acid oxidized components S and F.

Amino acid	Component S residues[1]	Component F residues[1]
Cysteic acid	6.0	6.0
Aspartic acid	22.6	21.7
Methionine sulfone	4.8	4.0
Threonine	10.3	8.0
Serine	19.7	13.1
Glutamic acid	31.2	31.5
Proline	10.6	7.4
Glycine	10.2	8.4
Alanine	15.7	10.3
Valine	9.0	5.6
Isoleucine	6.3	6.9
Leucine	25.8	20.6
Tyrosine	6.9	3.8
Phenylalanine	10.1	7.2
Histidine	6.5	4.7
Lysine	17.5	15.0
Arginine	14.0	7.5
Tryptophan[2]	2.1	2.1

[1] Based on 22,000 daltons for S and 20,000 for F.
[2] Spectrophotometric (Beaven and Holiday, 1952).

PEPTIDE MAPS

Figure 6 is a drawing of the peptide map obtained with component S. The F component gave an almost identical map but was different in that peptides labeled S were not seen and another peptide labeled F was noted.

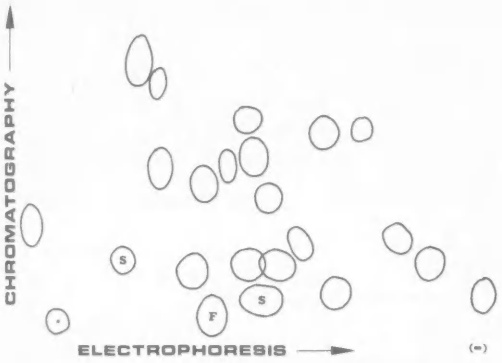

FIGURE 6.—Peptide map of a tryptic digest of component S. Chromatography was done with n-butanol-acetic-acid-water (4:1:5); electrophoresis was at pH 3.6 in a pyridine-acetic acid-water buffer (1:10:289). The peptide map of component F was identical except that peptides designated S were not seen and the peptide F was present.

DISCUSSION

From the immunodiffusion data we know that the S and F proteins are related to mammalian growth hormone. Their molecular weights also were near the values found for mammalian growth hormone and prolactin. One other observation which will be reported in detail later (Seavey et al., 1972)[6] was that the amino acid compositions of the tryptic peptides of the peptide maps closely resembled those of bovine growth hormone (Seavey et al., 1971). But because there were six half-cystine residues in both S and F and because each contained two residues of tryptophan, these two shark proteins are more like mammalian prolactins than the growth hormones which have only four half-cystines and one residue of tryptophan. Therefore, the proteins are not only very similar to each other, but are immunologically related to growth hormone and have structural resemblances to both growth hormone and prolactin. These results support the view that growth hormone and prolactin may have developed from a common ancestral protein. In the blue shark they appear as separate but yet quite similar substances with similarities to both growth hormone and prolactin. It will be interesting to see if there are two such proteins in the pituitary gland of cyclostomes.

If not already clear we would like to stress the point that no biological activities have been determined for the S and F components. Our assignment of growth hormone-like and prolactin-like properties are based on immunological and structural data alone. How these two components are related to the biological activities that have been reported for the shark pituitary gland is not known. Extensive biological studies are now needed to characterize these proteins. Also, more study will be given to the altered forms of the substances, and in particular the modification that was produced by incubation at 37°C. This type of study will be given to the altered forms of the hormones because of the rapid alterations that occurred even in the intact pituitary of the shark. We have observed that the prolactin activity of human growth hormone is increased when a hexapeptide is removed from the hormone by an enzyme present in pituitary extracts (Lewis et al., 1971). Biological activity of the shark hormones may also be affected by such changes. The nature of the alteration that occurs in the shark proteins is not known, but from our experiences with mammalian hormones we suspect that it is a result of deamidation, enzymic action, or a combination of both. The ease with which the shark's S and F components are converted to more acidic forms, however, strongly suggests deamidation, and the unusually large number of glutamic acid residues may actually be glutamines which rapidly lose ammonia.

ACKNOWLEDGMENTS

Much of this work was made possible by a grant from the National Institutes of Health (AM-09537). We also gratefully acknowledge the support given the project by the National Science Foundation in making the facilities of the RV *Alpha Helix* available for a 5-day cruise to study the pituitary of the blue shark. We are indebted to Dr. Y. N. Sinha of the Division

[6] Seavey, B. K., R. N. P. Sigh, U. J. Lewis, and R. Lasker. 1972. Tentative structure for a growth hormone-like, prolactin-like protein of the shark.

of Endocrinology, Scripps Clinic and Research Foundation, for the antisera used in these studies, and to Ronald Dotson and John LaGrange of the National Marine Fisheries Service for their assistance in catching the sharks.

ADDENDUM

The S component of the shark pituitary gland was tested for its ability to produce growth in hypophysectomized *Fundulus heteroclitus*. The results are shown in Figure 7. The preparation was found to be as potent as a previously assayed sample of hake growth hormone (Wilhelmi, 1955).

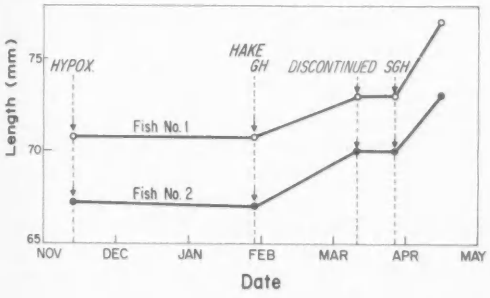

FIGURE 7.—Growth of two hypophysectomized male *Fundulus heteroclitus* after administration of growth hormone. Eleven weeks after hypophysectomy (HYPOX), injections of hake growth hormone (HAKE GH) (Wilhelmi, 1955) were begun and continued for five weeks. The injections were discontinued for two weeks and then resumed with shark growth hormone (SGH) for a period of four weeks. The S component of the shark pituitary gland was used. Both the hake and shark growth hormones were injected three times weekly at a dosage of 20 μg of hormone per gram (wet weight) of fish.

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DEVELOPMENT AND GEOGRAPHIC DISTRIBUTION OF THE ROCKFISH, *SEBASTES MACDONALDI* (EIGENMANN AND BEESON, 1893), FAMILY SCORPAENIDAE, OFF SOUTHERN CALIFORNIA AND BAJA CALIFORNIA

H. GEOFFREY MOSER[1]

ABSTRACT

The larval and juvenile stages of the scorpaenid fish, *Sebastes macdonaldi*, are described and illustrated. The sequence of ossification of bones and cranial spines in larvae is described in detail. *S. macdonaldi* appears to have the most southerly distribution of any species of *Sebastes* in the eastern north Pacific. The geographic distribution and seasonal abundance of *S. macdonaldi* larvae are discussed and compared with published information on the adults.

The genus *Sebastes* is represented by 65 species in the eastern north Pacific (Chen, 1971). Although all members of the genus are ovoviviparous and have a planktonic larval stage, they exhibit a remarkable diversity in morphology, color, and mode of existence. They rank first in total numbers of fish landed annually by the California sport fishing fleet (Young, 1969) and are a major commercial resource (Heimann and Frey, 1968). Despite their obvious importance, information on the complete life histories of all but a few species is fragmentary or nonexistent. At present a complete life history series (embryonic, larval, juvenile, and adult stages) has been described for only a single eastern Pacific species, *S. paucispinis* (Moser, 1967); however, young-stage larvae attained from pregnant females have been illustrated for four species from central California (Morris, 1956), for nine species from the Pacific northwest (DeLacy, Hitz, and Dryfoos, 1964), and for 14 additional rockfishes from southern California and Baja California (Moser, 1967). Recently, Waldron (1968) has described the early larvae of *S. pinniger*.

Ahlstrom (1961, 1965, 1969) has shown that rockfish larvae are the third or fourth most abundant kind of larvae collected annually in the plankton surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Early juvenile rockfish, like the larvae, are pelagic but evade plankton nets easily and must be collected by other means. For example, some species are attracted to bright lights at night and can be dipnetted at the surface. Also, some species associate with floating objects (Hitz, 1961) and with drifting kelp (Mitchell and Hunter, 1970) and may be collected when these are brought aboard ship. Finally, pelagic juveniles occasionally appear in midwater trawl samples (Berry and Perkins, 1966; Lavenberg and Fitch, 1966). Demersal juveniles are common constituents of otter trawl catches in coastal waters.

Larvae of *S. macdonaldi* have such a distinctive melanophore pattern that a developmental series was established before it could be identified to species. The extreme southerly distribution of these larvae in the CalCOFI pattern provided a clue to their identity, since adults of *S. macdonaldi* have been collected farther south along Baja California than any other species of *Sebastes* (Chen, 1971). A comparison of intraovarian larvae from pregnant *S. macdonaldi* with the smallest individuals from plankton collections provided definitive evidence of the identity of the larval series. Juvenile stages critical

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to the completion of the developmental series were obtained principally from midwater and bottom trawls. These developmental stages are described herein, with special emphasis on the developmental osteology of the larvae. Also, the geographic distribution of the larvae in the CalCOFI area is presented and compared with the known distributions of juveniles and adults.

METHODS

Larvae of *S. macdonaldi* from 4 years (1953, 1960, 1965, 1966) of CalCOFI survey cruises were identified and counted. From these and selected other specimens, two developmental series that encompassed the entire larval period were established. Larvae of the first series were measured with the ocular micrometer of a stereoscopic microscope to produce a table of morphometrics (Table 1) for comparison of body proportions of *S. macdonaldi* larvae with those of *S. paucispinis* and other species. This series also provided a framework for the descriptions of larval morphology and melanophore pattern. Larvae of the second series, cleared with a graded series of KOH-glycerin solutions and stained with Alizarin Red-S, were used to determine the sequence of ossification of bones and fin rays and to prepare a table of meristic characters (Table 2).

TABLE 1.—Measurements (mm) of larvae and pelagic juveniles of *Sebastes macdonaldi*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Snout-anus distance	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth	Pectoral fin length	Pelvic fin length	Snout to origin of anal fin	Snout to origin of pelvic fin
SIO 65-230	4.5	1.8	1.1	0.38	--	0.37	0.60	0.90	0.27	--	--	--
CalCOFI 6602-117.40	4.7	1.8	1.2	0.30	--	0.45	0.53	1.0	0.40	--	--	--
CalCOFI 6604-123.36	5.0	1.8	1.2	0.30	--	0.46	0.60	1.0	0.33	--	--	--
CalCOFI 6604-117.30	5.2	2.1	1.4	0.48	0.72	0.51	0.68	1.2	0.36	--	--	--
CalCOFI 6604-113.55	5.7	2.4	1.6	0.47	0.67	0.57	0.63	1.3	0.52	--	--	--
CalCOFI 6604-113.55	5.9	2.6	1.8	0.48	0.76	0.55	0.60	1.5	0.45	--	--	--
CalCOFI 6604-107.31	6.3	2.8	1.8	0.56	0.76	0.57	0.87	1.6	0.60	0.05	--	1.9
CalCOFI 6604-93.28	6.7	2.9	1.9	0.56	--	0.63	0.86	1.7	0.61	0.04	--	2.1
CalCOFI 6604-127.40	6.8	3.1	1.9	0.55	0.95	0.70	0.95	1.8	0.62	0.15	--	2.2
CalCOFI 6501-117.45	7.0	3.3	2.1	0.75	1.1	0.70	1.1	1.9	0.60	0.12	--	2.3
CalCOFI 5304-117.45	7.6	3.5	2.2	0.79	1.1	0.73	1.1	2.0	0.68	0.20	--	2.3
CalCOFI 6602-110.40	7.7	3.8	2.7	0.82	1.2	0.84	1.2	2.3	0.90	0.33	4.2	2.5
CalCOFI 6605-117.35	7.9	3.8	2.7	0.82	1.3	0.90	1.2	2.5	0.93	0.25	4.2	2.7
CalCOFI F-47-117.35	8.2	4.2	2.9	1.1	1.3	1.0	1.5	2.5	1.1	0.52	4.8	3.0
CalCOFI F-46-130.40	8.5	4.7	3.2	1.2	1.7	1.0	1.6	3.0	1.3	0.80	4.9	3.2
CalCOFI 5303-123.40	9.0	5.0	3.2	1.1	1.7	1.0	1.6	2.8	1.2	0.65	5.4	3.2
CalCOFI 6604-133.40	9.2	5.3	3.4	1.1	1.5	1.1	1.8	3.1	1.4	0.89	5.4	3.6
CalCOFI C-46-117.40	9.5	5.2	3.6	1.3	1.7	1.2	1.7	3.1	1.5	1.1	5.6	3.6
CalCOFI 6605-123.70	9.7	5.4	3.5	1.2	1.7	1.2	1.8	3.2	1.6	1.1	5.8	3.7
CalCOFI F-46-133.35	10.0	6.2	3.7	1.2	1.9	1.3	1.8	3.5	1.8	1.2	6.4	3.8
CalCOFI 6004-130.45	10.3	6.3	3.8	1.4	2.0	1.3	1.8	3.5	1.7	1.2	6.5	4.4
CalCOFI F-46-133.35	11.2	6.8	3.8	1.4	2.2	1.3	1.8	4.0	2.1	1.5	7.0	3.8
CalCOFI 5304-123.40	12.0	7.7	4.5	1.4	2.5	1.5	1.8	4.2	2.4	1.8	7.7	5.2
CalCOFI 6605-127.45	15.0	9.4	5.8	1.7	3.2	1.9	2.1	5.2	3.5	3.1	9.7	5.4
SIO 65-201	15.4	9.3	5.8	1.7	3.0	1.8	2.2	5.5	4.0	2.9	9.6	5.8
CalCOFI 6604-133.30	15.9	10.0	6.5	2.1	--	2.0	1.9	5.2	3.6	2.8	10.1	7.1
*SIO 61-299	22.6	14.0	8.4	2.7	3.6	2.3	2.5	7.5	6.7	4.8	14.7	9.3
*SIO 54-87	27.8	18.6	10.6	3.1	4.5	2.8	3.0	8.9	8.8	6.2	19.3	11.2
*SIO 69-232	29.2	19.1	10.8	2.9	4.8	3.2	2.9	10.0	9.8	6.5	19.9	11.7
*LACM 8821-9	32.7	20.7	11.8	3.2	4.9	3.6	2.9	10.1	9.7	--	20.8	12.2
*LACM 8821-9	34.5	20.9	11.8	3.2	5.2	4.0	3.2	10.5	10.6	7.7	21.4	12.7
*LACM 8821-9	38.8	25.0	12.8	3.2	5.4	4.0	3.5	11.7	11.2	8.3	25.6	14.4
*LACM 8821-9	40.2	26.8	13.0	3.5	6.1	4.2	3.6	12.0	12.2	8.5	27.4	15.2
*LACM 8821-9	44.4	30.2	14.0	3.8	6.4	4.7	3.8	13.2	13.2	9.2	31.2	16.2

* Pelagic juvenile.

TABLE 2.—Meristics from cleared and stained larvae of *Sebastes macdonaldi*.

Length (mm)	Primary caudal fin rays		Secondary caudal		Branchiostegal rays		Pectoral fin rays		Hypural elements		Dentary teeth		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebral centra	Neural spines	Haemal spines
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Left	Right			Left	Right			
6.3	--	--	--	--	2	2	2	2	--	--	--	--	--	--	--	--	--	--	--
6.7	--	--	--	--	3	3	3	3	--	--	--	--	--	--	--	--	--	--	--
6.8	--	--	--	--	3	3	3	--	--	--	--	--	--	--	--	--	--	--	--
7.0	3	3	--	--	4	4	6	6	--	--	--	--	--	--	--	--	--	--	2
7.1	4	3	--	--	5	5	6	6	--	--	--	--	--	--	--	--	--	4	--
7.2	3	3	--	--	5	5	--	8	--	--	--	--	--	--	--	--	--	4	--
7.7	6	6	--	--	6	6	11	11	--	--	--	--	--	--	I-0	I-0	5	12	--
7.9	4	4	--	--	5	5	9	10	--	--	--	--	--	--	--	--	3	6	--
8.2	8	7	2	2	7	7	17	17	--	--	--	--	iii-4	VII-0	I-3	I-3	24	20	7
8.5	7	7	--	1	6	6	15	15	--	1	--	--	--	--	I-3	I-3	18	18	6
8.7	8	7	--	1	7	7	16	16	--	--	--	--	--	IV-0	I-3	I-3	18	19	6
9.2	8	7	2	3	7	7	19	18	2	3	--	--	--	VII-8	I-4	I-4	23	21	9
9.4	8	7	4	4	7	7	19	19	2	3	--	--	III-7	XIII-13	I-5	I-5	24	23	13
9.7	8	7	3	4	7	7	19	19	2	3	--	--	III-7	XIII-13	I-5	I-5	24	23	12
10.0	8	7	5	6	7	7	19	19	2	3	4	5	III-7	XIII-13	I-5	I-5	24	23	14
10.3	8	7	5	5	7	7	19	20	2	3	4	4	III-7	XIII-13	I-5	I-5	26	24	14
11.3	8	7	4	4	7	7	19	19	2	3	5	5	III-7	XIII-13	I-5	I-5	26	24	14
12.0	8	7	8	7	7	7	19	19	2	2	3	2	III-7	XIII-13	I-5	I-5	26	24	14
15.0	8	7	10	11	7	7	19	19	3	2	11	13	III-7	XIII-13	I-5	I-5	26	25	14
15.9	8	7	10	11	7	7	19	19	3	2	12	10	III-6	XIII-12	I-5	I-5	26	25	14

The critical pelagic juvenile stages were found in the fish collections of the Scripps Institution of Oceanography (SIO) and the Los Angeles County Museum of Natural History (LACM). Demersal juveniles were obtained from bottom trawl collections of the Southwest Fisheries Center, La Jolla, and the University of California at Los Angeles (UCLA), in addition to the two sources mentioned above.

Prior to the completion of notochord flexion during caudal fin formation, the body length is defined as the distance from the tip of the snout to the posterior tip of the notochord. After notochord flexion is completed the usual standard length measurement, the distance from the tip of the snout to the posterior margin of the hypural plate, is used. Morphometric changes in rockfish can be conveniently grouped into three phases that correspond to the stages of notochord flexion—one before flexion, one during flexion, and one after flexion is completed. These stages are separated in the morphometric table. Other terms used in this table are defined as follows:

Snout-anus distance = distance along midline of body from tip of snout to vertical from anus

Head length = distance from tip of snout to cleithrum

Snout length = distance from tip of snout to anterior margin of eye

Upper jaw length = distance from tip of snout to vertical from posterior margin of maxillary

Interorbital distance = width of tissue dorsal to eyes

Body depth = body depth at base of pectoral fin

Pectoral fin length = maximum length of rayed portion of fin

Pelvic fin length = maximum length of rayed portion of fin

Snout to origin of anal fin = distance along midline of body from tip of snout to a vertical from anterior end of anal fin

Snout to origin of pelvic fins = distance along midline of body from tip of snout to a vertical from pelvic fin base.

Terms used in the description of larval osteology conform largely to those used in recent studies of the osteology of adult teleosts (e.g., Harrington, 1955; Weitzman, 1962; Topp and Cole, 1968).

DESCRIPTION OF DEVELOPMENT

DISTINGUISHING FEATURES

Early-stage larvae of *S. macdonaldi* are characterized by a low number of melanophores (average of eight) in the series along the ventral midline of the tail. Of the 27 other species illustrated in the literature, only *S. paucispinis* larvae, with an average of nine melanophores in this series, approaches the low number of *S. macdonaldi*. Early larvae of *S. macdonaldi* are also characterized by their small, densely pigmented pectoral fins. Melanophores cover completely the blade of the fin, but are restricted to the inner surface of the fin base. Also characteristic is the series of melanophores which extends from the nape to the pectoral fin base. Such melanophores are not present on any other of the 27 other eastern Pacific species illustrated to date.

A fourth character of limited utility is the absence of melanophores on the dorsal surface of the tail. *S. macdonaldi* is one of the 16 eastern Pacific species illustrated to date which lacks this pigment, and can be immediately separated from the 12 species in which it is present. This character should be used with caution because the dorsal series of melanophores forms later than the ventral series, at about the time of yolk depletion (Moser, 1967; Waldron, 1968). Thus, prolarvae collected prematurely from the ovaries may not have yet developed their dorsal pigment series, and illustrations of this stage are not strictly comparable with those of larvae cultured to the point of yolk depletion.

GENERAL MORPHOLOGY

Larvae of *S. macdonaldi* are similar in general appearance to those of *S. paucispinis* (Moser, 1967). Larvae hatch within the ovaries at a length of 4 to 5 mm, and then are extruded from the female. Newborn larvae have large heads with well-formed eyes and functional jaws (Figure 1A). The gut is short and bulbous; usually remnants of the yolk and oil globule are visible anteriorally in the region of the liver.

Relative body depth increases markedly during early larval stages and less so during later larval stages (Figures 1, 2). Body depth at the base of the pectoral fins averages 23% of the body length before notochord flexion, 33% during flexion, and 34% after flexion. In pelagic juveniles (Figure 3), relative body depth decreases slightly to about 30% in individuals 35 to 40 mm long. *S. paucispinis* is more slender throughout the larval and early juvenile stages; body depth averages 20% of the body length before notochord flexion, 24% during flexion, 31% following flexion, and 28% in pelagic juveniles.

Relative gut length increases gradually throughout the larval period. Accordingly, snout-anus length averages 42% of the body length before notochord flexion, 52% during flexion, 60% after flexion, 64% in pelagic juveniles. A similar gradual increase occurs in *S. paucispinis* (41, 44, 56, and 63% in the respective stages).

Relative head length increases slightly during the larval period; head length averages 28% of the body length before notochord flexion and 37% during and after flexion, but decreases during transformation and is 32% in the largest pelagic juveniles. Eye diameter averages 33% of the head length throughout the larval period and shows no trend of relative increase or decrease. Relative eye diameter decreases slightly to about 28% in transforming individuals, but increases to about 32% in the largest pelagic juveniles.

Upper jaw length is variable with respect to head length, probably because of the difficulty in obtaining uniform measurements from specimens with partially opened jaws. There is, however, a general trend of relative increase; jaw length averages 47% of head length before notochord flexion, 49% during flexion, and 52% in postflexion larvae. In large larvae and in pelagic juveniles the end of the maxillary is located beneath the middle of the orbit. With continued elongation of the maxillary in demer-

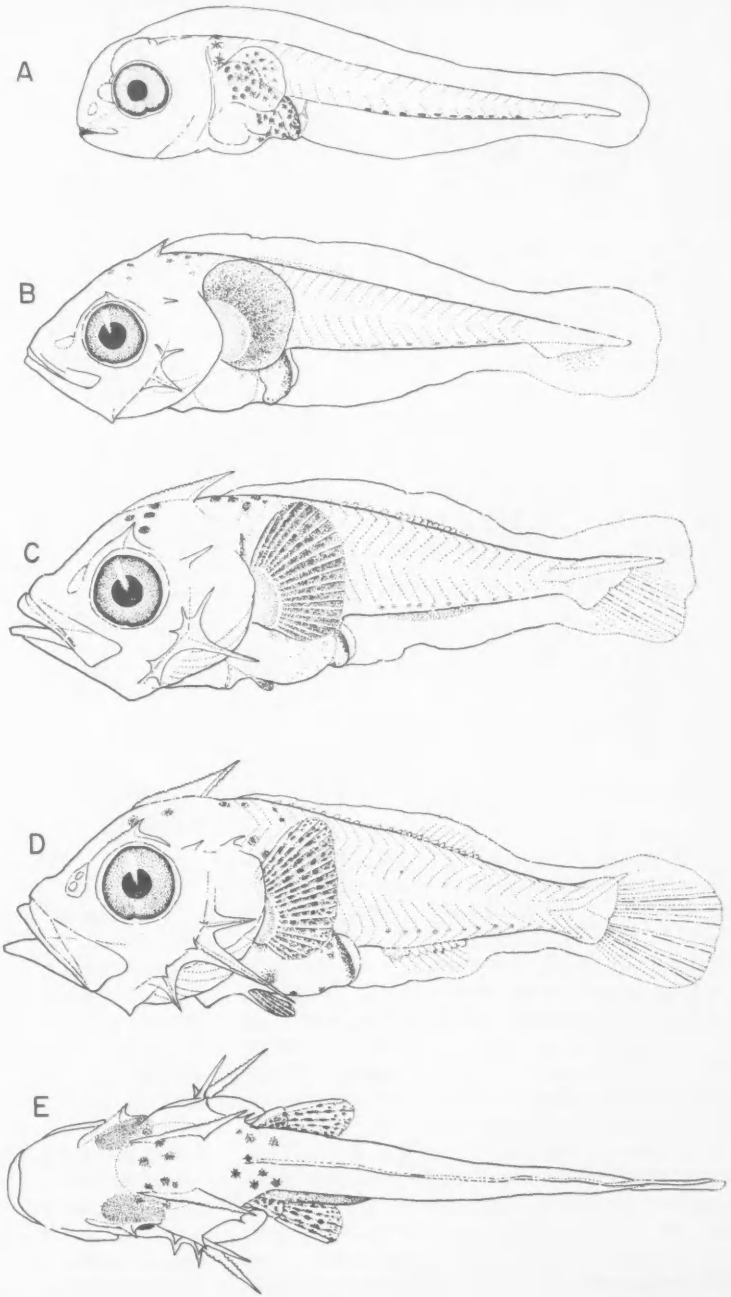

FIGURE 1.—Larvae of *Sebastes macdonaldi* from a pregnant female (A) and from California Cooperative Oceanic Fisheries Investigations (CalCOFI) plankton samples (B-E). A. 4.5 mm; B. 6.3 mm; C. 7.7 mm; D. 9.0 mm; E. dorsal view, 9.0 mm.

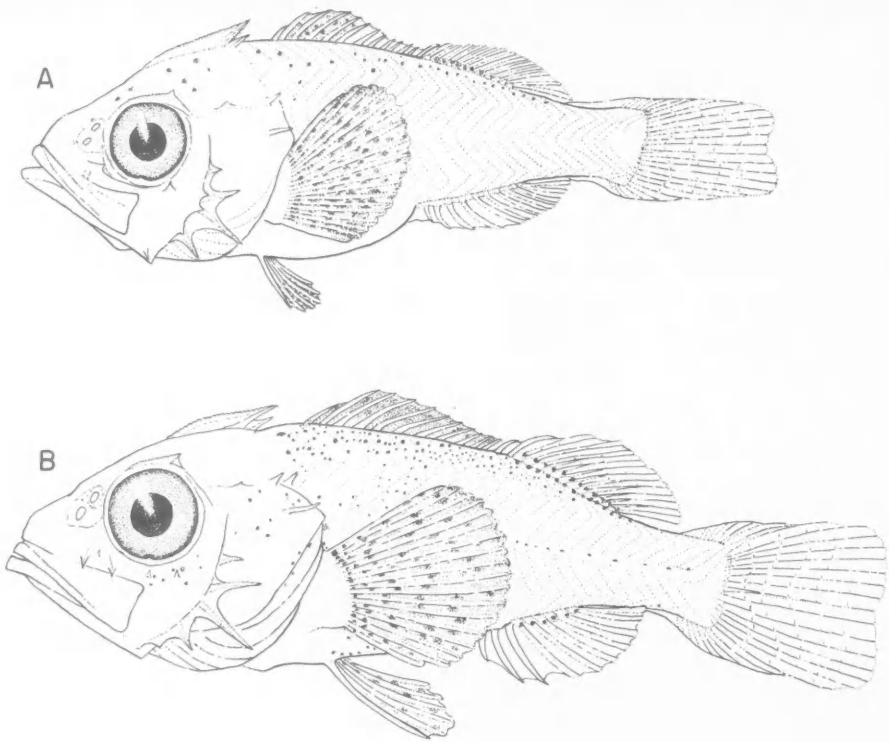

FIGURE 2.—Planktonic larvae of *Sebastes macdonaldi* from CalCOFI plankton samples. A. 11.2 mm; B. 15.9 mm.

sal juveniles (Figure 4) and in adults, its posterior end extends to below the posterior margin of the orbit. The relative length of the snout does not change markedly during the larval period; snout length averages 32% of the head length throughout the larval period. In pelagic juveniles snout length is reduced slightly to an average of 28% of the head length. Likewise, the width of the interorbital region changes little relative to head length in larvae; it averages about 46% of the head length. At the end of the larval period the interorbital distance becomes markedly narrower and averages 27% of the head length in pelagic juveniles. Similar changes in relative growth rate of the head, eyes, jaws, snout, and interorbital region occur in larvae and early juveniles of *S. paucispinis*.

FIN DEVELOPMENT

The pectoral fins begin to form during embryogenesis and, at parturition, the muscular base of each fin is distinct from the fan-shaped future rayed portion. The rayed portion enlarges considerably during early planktonic life and becomes covered solidly with melanophores (Figure 1B). The rays begin to ossify in larvae as small as 6.3 mm (Table 2); ossification begins with the most dorsal rays and then proceeds ventrad sequentially. Larvae 19.2 mm and larger have the full complement of 19 stained pectoral rays. The pectoral fins elongate slowly and gradually and have a short stubby appearance during most of the larval period. The length of the rayed portion of the fin averages 8% of

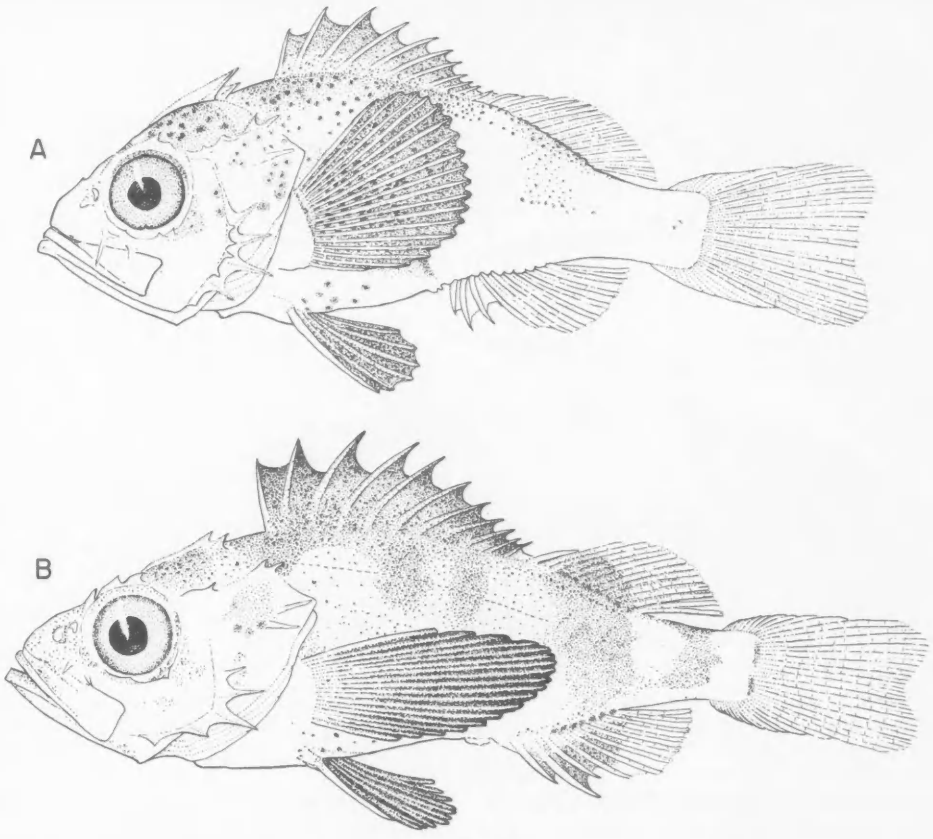

FIGURE 3.—Pelagic juveniles of *Sebastes macdonaldi*. A. A 15.4-mm transforming specimen (SIO 65-201, midwater trawl) which is just beginning to develop its juvenile melanophore pattern. Note that it is further advanced than the 15.9-specimen in Figure 2. B. A 29.2-mm specimen dipnetted on surface at night (SIO 69-232).

the body length in the stages before notochord flexion, 13% during flexion, and 19% in the stages following flexion. The fin elongates markedly in pelagic juveniles in which its average length is 31% of the body length (Figures 3B, 4A). This sequence of gradual elongation of the pectoral fins throughout the larval and early juvenile period contrasts with that observed in *S. paucispinis* (Moser, 1967). In that species, the maximum length of the pectoral fins, 40% of the body length, is achieved in 13-mm larvae and, thereafter, the pectoral fin length decreases relative to body length; pectoral fin length is 25% of the body length in newly transformed juveniles of *S. paucispinis*. In both species, the heavily pigmented pectoral fins are the most striking features of larvae and early juveniles.

The pelvic-fin buds appear early, in larvae as small as 6.3 mm, and become covered with melanophores. The rays begin to differentiate in 7-mm larvae. Ossification of the spines is visible initially in a 7.7-mm specimen in the stained series (Table 2). Ossification of the rays proceeds sequentially posteriad from the spines; the

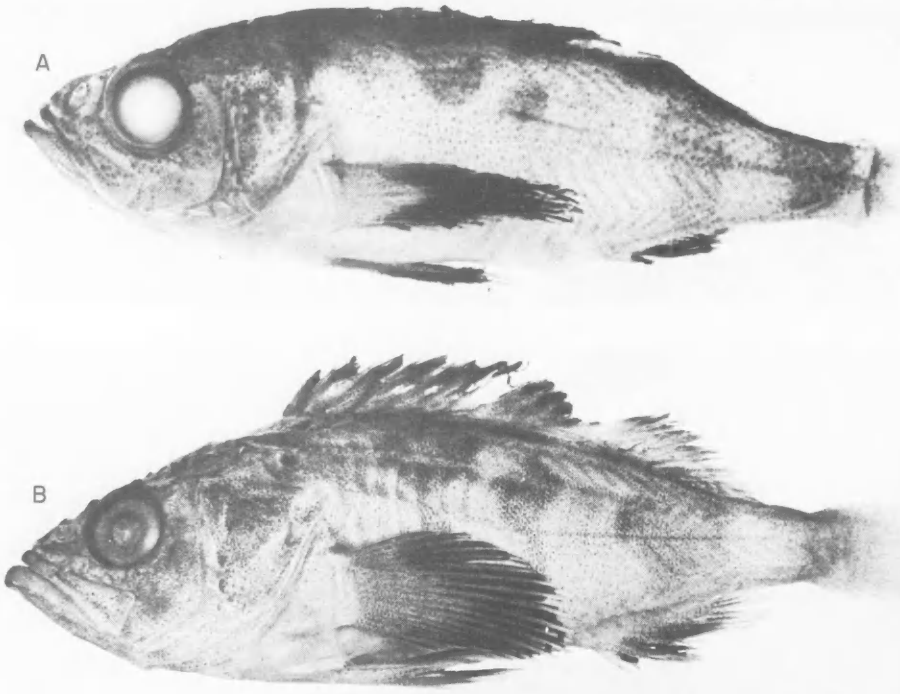

FIGURE 4.—Juveniles of *Sebastes macdonaldi*. A. A 40.2-mm pelagic juvenile (LACM 8821-9) collected by midwater trawl in the Gulf of California. B. A 62.1-mm demersal juvenile (SIO 65-227) collected by otter trawl near Point Tosco, Baja California.

full complement of five ossified rays is present in each fin in a 9.4-mm stained specimen. Like the pectoral fins, the densely pigmented pelvics elongate gradually throughout the larval period. Pelvic fin length increases from 4% of the body length at the initiation of notochord flexion to 10% at its completion. Following flexion, it increases gradually to a maximum of 18 to 21% of the body length in larvae 15.0 to 16.0 mm long. In pelagic juveniles pelvic fin length is 21 to 22% of the body length.

The caudal-fin anlage first appears in larvae about 5.0 mm long as a ventral thickening near the tip of the notochord. The cartilaginous hypural elements begin to differentiate when the larvae are about 6.0 mm (Figure 1B) and the maximum number of three superior and two inferior hypurals is present at about 8.0 mm. Ossification of these elements begins in larvae about 8.5 mm long and all hypurals, except the slender dorsal-most element of the superior series, are ossifying in a larva 9.2 mm long. Fusion accompanies further ossification in the superior series; in the largest larva the two larger superior elements have nearly fused into a single plate, while the slender uppermost element remains separate and has just started to ossify. In the inferior series the larger upper element has two centers of ossification which produce a solid calcified plate in the largest larva. The slender lowermost element is also well ossified but remains separate. Thus, larvae of 15-mm length have achieved the adult complement of two superior and two inferior hypurals. The principal caudal rays begin to ossify in 7-mm larvae (Table 2). Ossification proceeds dorsad in the superior series, above the midline of the fin, and ventrad in the inferior series; the adult complement of

8 + 7 principal rays is present in an 8.2-mm larva of the stained series. Also, the initial procurrent rays are ossifying in this specimen. Ossification of these rays proceeds anteriad in both superior and inferior series. The largest larva (15.9 mm) has 10 superior and 11 inferior ossified rays, but the full complement of 11 to 13 superior and 13 to 15 inferior rays is attained in pelagic juveniles.

The dorsal and anal fins are the last to appear. The bases of the fins appear in larvae 5.3 to 7.0 mm long (Figures 1B, C). Cartilaginous radial elements start to differentiate when the larvae are about 7.0 mm and the full complements of these elements are present in larvae 8.0 to 8.5 mm. Initial ossification of the spinous rays of these fins is visible in an 8.2-mm specimen in which the three anal spines and the anterior seven dorsal spines are stained. A larger, but apparently less advanced specimen, 8.7 mm long has only four stained dorsal spines and shows no stain on the anal spines. A 9.2-mm faintly stained larva has seven spinous and eight soft dorsal rays but shows no stain on the anal rays. The next larva in the stained series, 9.4 mm long, has the adult complement of III-7 anal and XIII-13 dorsal rays. The remaining larvae in the stained series, with the exception of one specimen, also have III-7 anal and XIII-13 dorsal rays.

PIGMENTATION

Newly hatched *S. macdonaldi* larvae have a melanophore pattern similar to that of *S. paucispinis*. The gut is covered with a mantle of melanophores that is solid on the dorsal surface and more sparsely distributed on the lateral and ventral surfaces (Figure 1A). A line of melanistic dashes on the ventral midline of the tail extends posteriad from the third or fourth postanal myomere. In a sample of 60 newborn larvae of *S. macdonaldi* the number of melanophores in the ventral midline series ranged from 6 to 14 with a median of 8. Thus, this species has fewer ventral midline melanophores than any eastern Pacific species of *Sebastes* studied to date (see Morris, 1956; DeLacy et al., 1964; Moser, 1967). Head pigmentation in newborn larvae consists of a series of melanophores that line the anterior region of the lower jaw and one to several melanophores that form a blotch on the nape. The pectoral fins also are pigmented; the inner surface of each fin base is covered solidly with melanophores while the lateral surface is pigmentless. The future rayed portion of the fin has sparsely distributed melanophores on both lateral and inner surfaces.

Melanophores are added throughout the larval period so that large larvae of *S. macdonaldi* are among the most heavily pigmented of all rockfish species (Figures 1, 2, 3). Much of the melanistic pigment is added in the head region. One or two melanophores appear over each optic lobe of the brain in 4- to 5-mm larvae. Similarly one or two melanophores appear above each side of the cerebellum in larvae of the same size. Melanophores are added continuously to the dorsal surface of the brain so that it is covered completely when the larvae reach 8.0 mm. Beginning in larvae about 7.0 mm long, isolated melanophores form anterior to the cleithra and eventually form a small patch that is covered by the opercle. When the larvae reach about 10.0 mm, considerably more pigment is added to the head. Patches of melanophores form around the external nares and along the anterior rim of the upper jaw; gradually the entire dorsal region of the snout becomes covered. Also, a conspicuous melanophore patch appears at the ventroposterior margin of the orbit and on the dorsal surface of the opercle.

Pigmentation on the gut, particularly on the dorsal and lateral surfaces, becomes more extensive during larval development. Beginning in larvae of about 5.0-mm length, melanophores are added in the region dorsal to the pectoral fin base and eventually a continuous band of melanophores extends from the gut to the enlarging melanistic blotch at the nape.

The number of melanophores in the series at the ventral midline of the tail appears to diminish as development proceeds; this may be an apparent reduction since the melanophores become embedded in the developing hypaxial musculature and later become obscured by the developing anal fin. Typically, in larvae larger than 8.0 mm the three posterior melanophores

in the series are visible along the ventral margin of the caudal peduncle while more anterior melanophores of the series are barely visible above the developing anal fin.

The paired fins are strikingly pigmented. Melanophores are added continuously to the rayed portion of the pectoral fin but are scattered until the larvae are about 7.0 mm long (Figure 1C) when they become concentrated on the membranous portions of the fins between the developing rays and give the fins a striated appearance that remains throughout the larval period. The base of the pectoral fin remains heavily pigmented only on the medial surface. Melanophores begin to appear on the pelvic fins in larvae about 7.0 mm long and form a striated pattern like the pectorals when the larvae reach a length of about 8.5 mm.

The median fins develop pigmentation considerably later in the larval period. When larvae reach about 9.0-mm length (Figures 1D, E), the melanophore patch on the nape begins to expand posteriad along the dorsal midline to form an elongated patch at the base of the spinous dorsal fin. A separate elongated patch of melanophores develops at the base of the soft dorsal fin and the two become connected by a narrow bridge of melanophores when the larvae reach about 10.0 mm. Melanophores begin to form on the anterior portion of the spinous dorsal fin when the larvae are about 9.0 mm long. Gradually the pigmented area of the fin enlarges until the entire spinous dorsal is pigmented in larvae longer than 15.0 mm (Figure 2B). Pigment on the soft dorsal fin is limited to a series of melanophores that covers the distal radial elements of the fin base. These melanophores begin to appear in 11-mm larvae and cover nearly all the radial elements when the larvae reach 15.0 mm (Figures 2A, B). A similar series of melanophores develops along the anal fin base when the larvae reach 12.0-mm length. One to several melanophores appear at the posterior margin of the hypural elements. In pelagic juveniles other melanophores are added here to form a vertical line (Figures 3B, 4A).

The beginnings of the juvenile pigment pattern appear in larvae 15.0 to 16.0 mm long when saddles of melanistic pigment start to develop ventrad from the elongate patches that lie along the dorsal fin base (Figures 2B, 3A). The first of these extends ventroanteriad from the origin of the dorsal fin to meet with the melanistic blotch on the opercle. A second saddle extends from the middle region of the spinous dorsal fin ventrad to overlie the lateral line, as does a third saddle which extends ventrad from the base of the soft dorsal fin.

These melanistic saddles become further developed in pelagic juveniles. In a 22.6-mm juvenile the pigment saddle at the soft dorsal fin extends almost to the base of the anal fin, and a fourth saddle is present at the caudal peduncle. In a 29.2-mm specimen (Figure 3B) the broad band at the soft dorsal is continuous and extends onto the rays of the dorsal and anal fins. The band at the caudal peduncle also extends to the ventral midline. Also, in this specimen, an additional saddle is present below the posterior end of the spinous dorsal fin, just posterior to the one located below the middle of the fin. In the largest pelagic juveniles (33-44 mm) the most anterior bar at the origin of the dorsal fin is obliterated as it becomes continuous with the solidly pigmented dorsal region of the head (Figure 4A). Melanistic pigment on the fins is augmented in pelagic juveniles. The entire spinous dorsal is dark and has a black margin whereas only the basal regions of the soft dorsal and anal fins are covered with melanophores. The caudal fin lacks melanophores. The pelvic fins remain pigmented as in late-stage larvae; however, a zone without melanophores develops on the basal third of each pectoral fin.

The melanistic pigment pattern of the smallest demersal juveniles (60 mm SL) remains essentially like that of pelagic juveniles (Figure 4). The smallest fresh specimens examined were 150 mm SL. In these the melanistic saddles and bands are separated by dusky areas above the horizontal septa. Below the septa, the background color is crimson, as is the lateral line and the head below the ventral markin of the orbit. The spinous dorsal fin is dusky with a black margin whereas the soft dorsal has a dusky base, a black central zone, and a pale margin. The caudal, anal, pelvic, and pectoral fins have crimson rays alternating with black between the rays.

In large adults the lateral melanistic patches and bands coalesce to form a solid black zone above the horizontal septa with a crimson zone below. At least the posterior half of the lateral line remains bordered by crimson. The spinous and soft dorsal fins become black. The caudal fin is black except for a vertical crimson zone at the base. The anal and ventral fins remain crimson with black between the rays. The pectoral fins become black except for a red zone at the proximal third of each fin.

SEQUENCE OF OSSIFICATION

The sequence of calcification of bones in larvae of *S. macdonaldi* is similar to that described for larvae of Myctophidae (Moser and Ahlstrom, 1970). As in myctophids, the maxillaries and cleithra are the first elements to ossify. In fact, the maxillaries, cleithra, and opercles are beginning to ossify in full-term intraovarian larvae. The sequence of ossification of other head, appendicular, and axial elements in a stained series of *S. macdonaldi* is shown in Table 3. For each element, the larval length at initial ossification and the larval length at which the element achieves its adult form are given. Selection of the point at which an element achieves its adult form, admittedly, is somewhat subjective since bone formation is a gradual process that continues throughout the life of the fish. In rockfish, as in most other teleosts, most of the skeletal elements become ossified during the larval period and assume a shape which, except for minor surface irregularities and processes, closely resembles that found in juveniles and adults. The branchial arches and cranial spines ossify gradually and generally have not achieved their adult form before the end of the larval period. For this reason these are listed in separate tables (Tables 4, 5), which give only the sequence of initial ossification.

Although the neurocranium is unossified in unborn larvae, the frontals, pterotics, and parasphenoid form soon after birth, in larvae 5.1 to 5.2 mm. These are followed by the parietals, exoccipital, bosioccipital, and supraoccipital, and later the circumorbital bones and the more interior neurocranial elements.

In the upper jaw the maxillaries begin to ossify before birth. These are followed by the main elements of the lower jaw, the dentaries and articulars, which begin to ossify at 5.1 to 5.2 mm. Other elements of the jaws, the premaxillaries and angulars, are beginning to ossify in a 6.3-mm stained larva. All elements of the mandibular arch achieve their adult form early in the larval period, between 7.0 and 8.5 mm. The elements of the palatine series are slower to ossify. The quadrates begin to ossify at about 6.3 mm and the others follow gradually; the last elements to initiate ossification, the palatines and metapterygoids, achieve their adult form in 12.0-mm and 15.9-mm larvae respectively.

The bones of the hyoid arch and opercular series initiate ossification gradually, beginning with the opercle in unborn larvae. The other bones of the opercular series have started to ossify before the larvae reach 6.3 mm, and all have achieved their adult form at 7.9 to 8.2 mm. Elements of the hyoid arch, particularly the ceratohyals and interhyals, are slower to initiate and complete ossification.

In the appendicular skeleton, the cleithra are the first bones to become ossified. They are heavily stained in unborn larvae and are the first skeletal elements to ossify. Following birth, the other bones of the pectoral girdle gradually initiate ossification. Among the last to appear are the four proximal radial elements, which ossify in a dorsal-to-ventral sequence. The coracoids and the single pair of extrascapulars initiate calcification at about 12.0 mm and are formed in the 15.9-mm specimen. The pelvic bones appear initially in a 9.2-mm stained specimen; through gradual ossification the pelvics become fused along their medial surfaces.

The paired neural arch elements are the first bones of the axial skeleton to ossify. At first only the most anterior pair is visible in a 7.0-mm larva, but gradually others are added in a posteriad sequence. When the larvae are about 8.0 mm long, the distal ends of each pair begin to fuse in the midline to complete the neural arch. This fusion and the resultant formation of a neural spine on each arch also occurs in an anterior to posterior sequence. The full complement of neural spines, including a shortened one

TABLE 3.—Sequence of ossification in larvae of *Sebastes macdonaldi*. The initial ossification of an element is indicated by "X" and the point of the arrow indicates the larval size at which the element achieves the general shape it will have in the juvenile and adult.

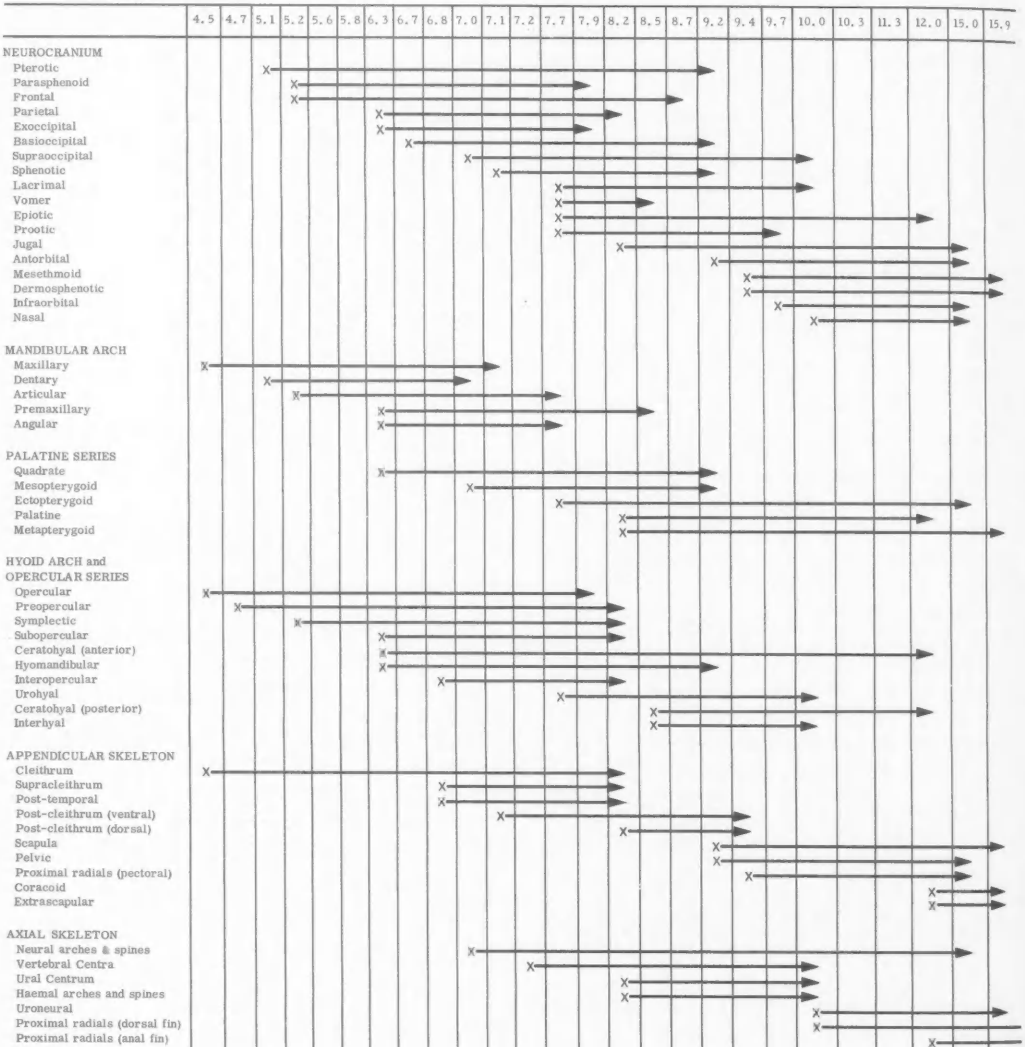

TABLE 4.—Sequence of initial ossification of branchial arch elements in larvae of *Sebastes macdonaldi*.

Element	Larval length at initial ossification (mm)
Pharyngobranchial teeth (3rd arch)	4.7
Ceratobranchial (1st arch)	6.3
Ceratobranchial (2nd arch)	6.3
Ceratobranchial (3rd arch)	6.3
Ceratobranchial (4th arch)	6.7
Ceratobranchial gill rakers (1st arch)	6.7
Ceratobranchial gill rakers (2nd arch)	7.2
Epibranchial (1st arch)	7.2
Epibranchial (2nd arch)	7.2
Ceratobranchial teeth (5th arch)	7.2
Ceratobranchial (5th arch)	7.7
Epibranchial (3rd arch)	7.7
Pharyngobranchial teeth (4th arch)	7.7
Ceratobranchial gill rakers (3rd arch)	7.7
Epibranchial gill rakers (1st arch)	8.2
Epibranchial (4th arch)	8.2
Hypobranchial (1st arch)	8.7
Epibranchial gill rakers (2nd arch)	8.7
Basibranchials	9.2
Hypobranchial (2nd arch)	9.2
Hypobranchial (3rd arch)	9.4

TABLE 5.—Sequence of initial ossification of head spines of larvae of *Sebastes macdonaldi*.

Spine	Element	Size of specimen at initial appearance (mm)
Pterotic	Pterotic	5.1
Preopercular, 3rd, posterior series	Preopercular	5.1
Preopercular, 4th, posterior series	Preopercular	5.2
Parietal	Parietal	6.3
Postocular	Frontal	6.3
Preopercular, 1st, anterior series	Preopercular	6.3
Preopercular, 2nd, anterior series	Preopercular	6.3
Preopercuiar, 3rd, anterior series	Preopercular	6.3
Preopercular, 2nd, posterior series	Preopercular	6.7
Supracleithral	Postemporal	7.7
Suborbital, 1st, inferior series	Lacrimal	8.2
Suborbital, 1st, superior series	Lacrimal	8.2
Preopercular, 1st, posterior series	Preopercular	8.2
Nuchal	Parietal	8.2
Opercular, 1st	Opercle	8.2
Opercular, 2nd	Opercle	8.2
Preopercular, 5th, posterior series	Preopercular	9.4
Suborbital, 3rd, superior series	Jugal	9.4
Cleithral	Supracleithrum	12.0
Nasal	Nasal	15.0
Suborbital, 2nd, inferior series	Lacrimal	15.0
Suborbital, 2nd, superior series	Infraorbital	15.0
Preocular	Antorbital	22.6
Supraocular	Frontal	22.6
Tympanic	Frontal	22.6

on the ultimate preterminal vertebra, is present in a 15.0-mm stained specimen.

The next elements of the axial skeleton to appear are the vertebral centra. The most anterior centra begin to ossify in larvae about 7.2 mm long. Ossification within each centrum begins at the bases of the neural arch and spreads mesially to form a straplike bridge between the bases. A similar structure forms ventrally between the bases of the haemal arch and ultimately the two bridges are joined by lateral ossification, to produce a complete central ring. This process proceeds in a posteriad sequence until the full complement of 25 central rings is attained in larvae of about 10.0 mm. Ossification of the ural centrum begins in an 8.2-mm specimen with the formation of two tandem osseus plates on each lateral surface. These spread rapidly to cover the entire lateral and dorsal surface of the centrum. Ossification of two ventral unossified regions is completed at about 10.0 mm to coincide with the formation of the ultimate preterminal centrum.

Haemal arches begin to ossify at about 8.2-mm length in a manner similar to that of the neural arches. Closure of the haemal processes into arches and the formation of haemal spines proceeds posteriad sequentially; when completed at 10.0 mm, vertebrae 1 to 4 are without haemal processes, 5 to 9 have unfused haemal processes, 10 and 11 have haemal arches without spines, and 12 to 25 have arches and spines.

All of the remaining major axial elements begin to ossify in larvae 10.0 mm or longer. The uroneurals appear as a pair of slender elements above the terminal centrum in a 10.0-mm specimen; they remain paired and sliverlike throughout the larval period. The proximal radial elements of the dorsal fin also begin to ossify at 10.0 mm and those of the anal fin at 12.0 mm, both in a posteriad direction; neither series is completed by 15.9 mm. A single interneural appears slightly above and in advance of the first neural spine in a 15.0-mm larva. Also, in this specimen the most anterior few ribs have just begun to ossify.

Several generalizations can be made from the information listed in Table 3. It is obvious that the various skeletal elements begin to ossify over a wide range of larval sizes and that the elements vary greatly in the time required for each to attain its adult form. For example, in the neurocranium, the jugal (third circumorbital) is formed over a span of nearly 7.0-mm length (8.2-15.0 mm) while the vomer begins to ossify

and achieves its adult shape over a span of about 1.0 mm (7.7-8.5 mm). Similar variation is found in the mandibular, palatine, and hyoid arches and in the axial and appendicular skeletons. Another less obvious generalization from Table 3 is that functionally related contiguous elements tend to achieve their adult form at about the same larval stage, regardless of when they underwent initial ossification. For example, the first six bones listed in the table are the major elements of the roof, sides, and floor of the brain case. Although they undergo initial ossification in a gradual sequence, all achieve their adult form in larvae 7.9 to 9.2 mm long. The bones of the opercular series (opercular, preopercular, subopercular, interopercular) begin to ossify in successive stages, but all achieve adult form at about the same stage. The pectoral girdle provides two excellent examples of this tendency in the cleithrum-supracleithrum-postemporal series and the scapula-proximal radial-coracoid series. Finally, there is no correlation between sequence of ossification and the origin (endochondral or dermal) of a bony element. Thus, of the first six elements of the neurocranium mentioned above, half are endochondral and half are dermal in origin. Here, the early appearance of these elements appears to be related to function and not to the kind of bone formed.

Analysis of the sequence of ossification of branchial elements is difficult since ossification is so gradual that one cannot choose a larval stage at which a given element achieves its basic adult form. Accordingly, only the larval size at which an element begins to ossify is listed in Table 4. As in other teleosts examined by me, the first bony structures to ossify in the larvae are the pharyngobranchial teeth. In *S. macdonaldi*, the tooth patches of the third pair of pharyngobranchial elements appear in the smallest planktonic larvae and enlarge throughout the larval period. In larvae of the Myctophidae it is the tooth patches of the fourth pharyngobranchials which ossify first (Moser and Ahlstrom, 1970). Aside from this, the sequence of ossification is similar in *Sebastes* and Myctophidae. The ceratobranchials are the first elements of the arches to ossify. These are followed by the epibranchials and hypobranchials, generally in an anterior to posterior sequence, beginning with those of the first arch. The first gill rakers to form are those on the first pairs of ceratobranchials and epibranchials and, gradually, they appear on more posterior arches. Within each arch, ossification proceeds outward from the angle of the arch. The full complement of rakers on the first arch is not achieved during the larval period.

Head spines present a special problem since some of the spines formed during the larval period are not found in adults. The terminology of Phillips (1957) is used in the discussion that follows. The first spines to form on the neurocranium are on the pterotic bones (Table 5). Interestingly, these spines begin to ossify before the bones themselves, and ossification of the bones spreads outward from the base of each spine. The spines are at first acute, but broaden during the larval period to produce a pterotic shelf in the largest larvae. The spine and shelf become reduced in pelagic juveniles and are absent in demersal juveniles and in adults. The two other pairs of spines which develop early in the larval period are the parietals and postoculars. The paired parietal spines develop as the terminal points of a pair of serrated parietal ridges and attain their maximum relative length (20-23% of the head length) in larvae 8.0 to 10.0 mm long. The ridges and their spines become reduced during later larval stages but remain in juveniles and adults. The postoculars develop from lateral shelves of the frontal bones that project over the eyes. Initially the spines are positioned directly above the eyes but gradually shift posteriad to their adult position. Preocular, supraocular, and tympanic spines do not form during the larval period; they are beginning to form in a pelagic juvenile 22.6 mm long and are well formed in the largest pelagic juveniles.

Other prominent cranial spines which develop later in the larval period are the suborbitals, nuchals, and nasals (Table 5). The suborbital spines form in two series: one series of ventrally directed spines develops on the ventral margin of each lacrimal (first circumorbital) bone and another series of laterally directed spines forms directly below the orbit. This lat-

ter series, composed of a single spine on each lacrimal, infraorbital, and jugal element, forms a shelf in late-stage larvae and in juveniles, but usually only the lacrimal spine remains in adults. The inferior series persists in adults and typically contains 3 to 5 spines. A nuchal spine forms directly posterior to each parietal spine in larvae about 8.0 mm long and persists in juveniles and adults. Nasal spines are late to form (15.0 mm) but also persist in adults.

Two spines appear on each preopercle in larvae 5.1 to 5.2 mm long. These are the third and fourth members of a series of five preopercular spines that forms throughout the larval period (Table 5). The third preopercular spines develop three longitudinal serrated ridges and elongate rapidly to become the longest larval spines. They reach a maximum length of 35% of the head length in larvae about 9.0 mm long and then decline in relative length. The five preopercular spines remain in juveniles and adults, but the short spines which develop immediately anterior to the second, third, and fourth preoperculars (Table 5) become obsolescent after the larval period. A pair of spines forms at the posterior margin of each opercle and persists in juveniles and adults.

The supracleithral and cleithral spines develop during the larval period; the supracleithral spines form on the postemporal elements in larvae about 7.7 mm long and the cleithral spines form on the supercleithra at about 12.0 mm. Both pairs persist into the adult stage.

DISTRIBUTION

S. macdonaldi has the most southerly distribution of any species of *Sebastes* in the eastern north Pacific. Chen (1971) lists its southern range record as Morgan Bank off Baja California (lat 23°24.0′N, long 111°11.5′W) and reports on the capture of a single adult specimen (LACM 8837-4) from Santa Inez Bay in the Gulf of California (lat 26°59.1′N, long 111°48.9′W). A collection of six pelagic juveniles (32.7-44.4 mm SL; LACM 8821-9) by midwater trawl from the Ballenas Channel in the Gulf of California (lat 28°56.5′N, long 113°10.5′W) is reported herein. Although the localities at Morgan Bank and Santa Inez Bay are separated by a distance of approximately 1,000 km, it is likely that future collections in this region will substantiate Chen's (1971) suggestion that the outer coast and Gulf of California populations are continuous.

The southerly distribution of *S. macdonaldi* is shown by the distribution of the larvae (Table 6, Figure 5). For the 4 years examined, larvae were taken as far north as CalCOFI line 90 and as far south as line 137. Line 90, running southwesterly from Dana Point, Calif., probably delimits the northern extent of reproduction for this species, although an adult has been taken as far north as Pt. Sur, Calif. (Phillips, 1961). Total numbers of larvae and frequency of occurrence of larvae increase to the south of line 90.

FIGURE 5.—Stations at which larvae of *Sebastes macdonaldi* were collected during 4 years (1953, 1960, 1965, and 1966) of CalCOFI plankton surveys. Solid circles indicate stations where number of *Sebastes macdonaldi* larvae exceeded mean number (4.8) for all positive stations. Area of frequent occupancy is outlined (see Ahlstrom, 1961, for complete grid).

TABLE 6.—Total numbers of *Sebastes macdonaldi* larvae taken on 14 CalCOFI lines for 4 years (1953, 1960, 1965, and 1966) and abundance of larvae of this species compared with the total numbers of *Sebastes* larvae taken in hauls containing *S. macdonaldi*.

CalCOFI line	Latitude[1]	Total number stations occupied	Total stations containing *S. macdonaldi*	Percentage of positive stations to total stations	Number of *S. macdonaldi* larvae	Total number of *Sebastes* larvae in hauls containing *S. macdonaldi*	Percentage *S. macdonaldi* larvae of total *Sebastes* larvae in hauls positive for *S. macdonaldi*
90	33°28.5′	383	1	0.26	1	31	3
93	32°56.0′	380	1	0.26	1	4	25
97	32°17.5′	325	1	0.31	1	28	4
103	31°07.0′	283	4	1.41	9	226	4
107	30°27.9′	273	8	2.93	12	226	5
110	29°52.0′	306	9	2.94	17	202	8
113	29°24.2′	283	19	6.71	47	285	16
117	28°58.0′	315	47	14.92	289	968	30
120	28°25.0′	365	33	9.04	110	332	33
123	27°26.2′	198	28	14.14	151	613	25
127	26°57.5′	202	33	16.34	143	252	57
130	26°33.5′	243	22	9.05	37	100	37
133	26°08.5′	209	23	11.00	207	224	92
137	25°36.1′	214	15	7.01	39	45	87

[1] Latitude of most shoreward station of each CalCOFI line.

They attain their largest numbers from line 117 to line 127 (Cedros Island to San Hipolito Point) and then decrease to line 137. In contrast, for those hauls containing *S. macdonaldi*, the ratio of this species to the total number of *Sebastes* larvae in these hauls increases continuously southward. *Sebastes* larvae were not taken on lines south of 137, probably because of the infrequent occupancy of these lines. Reproduction of *S. macdonaldi* occurs as far south as Morgan Bank (between lines 147 and 150), since one of the two specimens collected there was a term female with viable larvae.

The seasonal abundance and size of *S. macdonaldi* larvae at all CalCOFI stations during 1953 and 1960 are shown in Table 7. Larvae began to appear in January, increased in numbers in February, and reached a peak in March. Abundance declined progressively from April to June. The mean length of the larvae increased slightly during the 6-month period and the largest larvae were collected from March to June.

The larval stage is ended at about 16 mm; indeed, a 15.4-mm specimen is already beginning to develop the juvenile melanophore pattern and the juvenile arrangement of cranial spines. The pelagic juveniles are rare in plankton collections, probably because of their ability to avoid plankton nets. Also, they may occur deeper than 140 m, the usual maximum depth of CalCOFI plankton tows. Nevertheless, a number of pelagic juveniles, 22.6 to 44.4 mm long, were captured by plankton net, midwater trawl, and dip net. These are listed in Table 1 and discussed in the previous section of the paper. The smallest juvenile collected by bottom trawl was 59.3 mm. This suggests that the transition from pelagic to demersal habitat occurs in the size range of about 45 to 60 mm. Demersal juveniles 60 to 100 mm are captured typically at a depth range of 80 to 100 m. With further growth they appear to seek deeper habitats as there is a trend for larger fish to be collected from greater depths. The largest specimen examined (532

TABLE 7.—Numbers (A), mean length in mm (B), and size range in mm (C) of *Sebastes macdonaldi* larvae taken during 2 years of the California Cooperative Oceanic Fisheries Investigations (CalCOFI).

Year	CalCOFI lines	JANUARY			FEBRUARY			MARCH			APRIL			MAY			JUNE		
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
1953	97-107	2	4.2	4.2	4	4.2	4.2-4.3	0	0	0	1	4.8	4.8	0	0	0	0	0	0
	110-120	5	4.3	3.8-5.3	19	4.5	3.5-7.1	138	5.0	3.3- 9.5	26	6.2	3.7-10.0	4	4.8	3.8-6.2	0	0	0
	123-137	13	4.4	3.3-3.5	20	4.6	3.9-8.7	143	4.8	3.3-11.2	34	5.3	3.8- 8.8	5	5.4	3.3-9.6	0	0	0
1960	97-107	0	0	0	6	5.1	4.3-6.5	6	5.6	4.7- 8.2	2	4.9	4.9	0	0	0	0	0	0
	110-120	0	0	0	12	4.7	4.4-5.2	81	5.2	3.8- 8.8	25	4.8	4.0- 6.2	4	5.3	4.5-7.3	5	4.3	3.7-5.8
	123-137	1	4.2	4.2	14	4.9	4.0-5.8	184	4.7	3.4-10.8	76	5.2	3.2-10.3	17	5.1	4.1-9.6	1	6.0	6.0

mm SL, SIO 65-126) was taken by hook and line at 256 m.

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CYCLING OF ELEMENTS IN ESTUARIES

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ABSTRACT

Meaningful evaluation of the ecological stresses imposed by man's release of heavy metals or radioisotopes into estuaries requires an improved understanding of the interactions between the waste materials and the functional components of the ecosystem. In this paper, we review and discuss the types of information required for the development of useful models for the cycling of contaminant metals (both radioactive and stable) in estuarine ecosystems. With particular reference to the coastal plain estuaries of the southeastern United States, we discuss the major reservoirs of those metals, the mechanisms and pathways of elemental transformation and rates of elemental turnover among reservoirs, and the responses of these processes and reservoirs to environmental change. A conceptual systems model is presented as the preliminary phase in the development of dynamic mathematical models of elemental cycling.

Estuaries form the interface between the open ocean and man's land base, which in the coastal zone undergoes intensive development to facilitate maximum use of the sea. This narrow interface is a highly productive environment used at some stage of development by most of the marine fishery organisms exploited by man. Waste products of man's expanding population and increasing industrialization are transported into and through this estuarine environment and may render the habitat unsuitable for desirable species, or may render certain species unfit for human consumption. Man's impingement upon estuaries has assumed many forms; estuarine habitats have already succumbed to industrial and municipal pollution, to landfill and dredging operations; and economic and population pressures demand that additional estuarine areas be challenged by an increasing multiplicity of additions and modifications whose combined ecological effects are yet unknown.

Meaningful evaluation of the ecological stresses imposed by man's activities requires an improved understanding of the interactions between the wastes and the functional components of the ecosystem. Such understanding entails knowledge of the general principles of ecosystem operation, and not merely a description of the ecosystem structure at one or more instants in time. Man's continued and expanding variety of demands on estuarine environments as producers of food, avenues of transportation, receptacles for wastes, and as sources of recreational and esthetic pleasure make it imperative that we understand the interactions of all the material imports, whether of human or natural origin; and all the outputs, including both tidal exports and human exploitation of resources, to ensure the continued viability of the resultant ecosystems. No estuarine ecosystem has yet been studied in sufficient detail to permit accurate prediction of ecosystem response to contaminative additions. Considerable insight may be gained, however, from attempts to synthesize adequate predictive systems models from fragmentary data already available from ecological studies, experimental biology, and experience with previous instances of pollution. In this paper, we examine and discuss briefly the nature of the information required for the development of useful models for the cycling of contaminant metals (both radioactive and stable isotopes) in estuarine ecosystems.

To understand the "cycling of elements" in a natural ecosystem necessitates identifying the major reservoirs of those elements, determining

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the mechanisms and pathways of elemental transformations and rates of elemental turnover among reservoirs, and determining the response of these processes and reservoirs to changes in the environment under study.

In aquatic ecosystems, nearly all of the metallic elemental content of the system resides in the sediments and in the water. The fraction residing in the biota is small—with phytoplankton and zooplankton constituting the most important living elemental reservoirs in terms of turnover and total physical transport and redistribution processes. The major commercial species harvested by man from estuaries have little effect on the overall distribution of metallic elements in the estuary, simply because most of these species are high in the trophic scheme and have relatively low biomass. Yet, in contaminated environments these same species may concentrate certain elements to levels potentially harmful to people consuming large quantities of seafood. Our consideration of elemental cycling must therefore be biased toward biological species of little importance to the overall elemental mass balance because these species form the major interface between man and the remainder of the ecosystem.

METALLIC ELEMENTS OF PRIMARY CONCERN

In the preceding and ensuing paragraphs we discuss the cycling of "metallic elements." Such a generalization is not entirely practical because chemical and physical characteristics of the different metals determine to some extent their behavior in the natural environment and their relative toxicity to biological systems influences the extent of our interest in the various metals. In addition, the relative abundance of various elements affects both their ecological behavior and human interest. In terms of chemical and physical properties, we can categorize the metals into five groups: alkali metals, alkaline earths, transition elements, rare earths, and actinide elements. The transition elements may be further subdivided into "family groups" on the basis of the electronic configurations of the atoms. The term "heavy metal" usually refers to all those metals with atomic numbers higher than 20 (Ca), i.e., beginning with the first transition series: Sc, Ti, V, Cr, etc. In the popular literature "heavy metal" frequently also carries the connotations of pollution and/or toxicity. Table 1 categorizes metallic elements according to biological function and abundance and shows elemental abundances for seawater and the crust of the earth. Not all the elements listed in Table 1 as "essential" are required by every animal and plant—only a few higher plants may require aluminum or vanadium, silicon is an essential bulk component of diatoms not required by other forms, and molybdenum appears to be essential only to organisms that derive their nitrogen by nitrate reduction or fixation of free nitrogen (Underwood, 1962; Epstein, 1965). Similarly, the designation of toxicity is arbitrary, since most of the essential elements are toxic at unusually high concentrations. The nonessential elements include a few (cesium, rubidium, strontium) which consistently occur in organisms and can replace to a large degree the biological functions of essential elements (Rb and Cs for K, Sr for Ca). To a much lesser extent, the metals Cr, Ni, and Cd may fulfill the biological functions of Zn, Mn, or Cu. It should be noted that the metals which are essential or relatively nontoxic to biological systems generally have a low atomic number (only Rb, Sr, Mo, and Cs exceed 30) and are relatively abundant in the biosphere. The toxic metals generally have high atomic numbers (an outstanding exception is Be with an atomic number of 5) and low abundances (notable exceptions include As, Ba, and Pb, all of which occur consistently in living organisms, and Be and Th, which are extremely variable in their biological distribution).

In addition to the elements in Table 1, certain other metals are of concern because of radiation from radioisotopes, whether naturally occurring or introduced from man's nuclear activities. The abundances and composition of radionuclides in the marine environment are summarized elsewhere (Rice and Wolfe, 1971; Joseph et al., 1971). Most of the significant radionuclides are isotopes of certain elements in Table 1 such as chromium, iron, manganese, zinc, cesium, and strontium. To this list we should add cerium,

TABLE 1.—Metallic elements of biological significance.

	Seawater abundance[1]	Crust abundance[2]
	mg/liter	*ppm*
"Essential bulk" elements		
Calcium	400	36,300
Magnesium	1,350	20,900
Potassium	380	25,900
Sodium	10,500	28,300
"Essential trace" elements		
Cobalt	0.0005	23
Copper	0.003	45
Iron	0.01	50,000
Manganese	0.002	1,000
Zinc	0.01	65
Aluminum	0.01	81,300
Molybdenum	0.01	1
Silicon	3	277,200
Vanadium	0.002	110
"Nonessential trace" elements		
Cesium	0.0005	1
Chromium	0.00005	200
Nickel	0.002	80
Rubidium	0.12	120
Strontium	8	450
Tin	0.003	3
"Toxic" elements		
Antimony	0.0005	0.2
Arsenic	0.003	2
Barium	0.03	400
Beryllium	0.0000006	2
Bismuth	0.00002	0.2
Cadmium	0.00011	0.2
Lead	0.00003	15
Mercury	0.00003	0.5
Selenium	0.004	0.09
Silver	0.0003	0.1
Thorium	0.00005	10

[1] Goldberg, 1963.
[2] Mason, 1958.

zirconium, niobium, ruthenium, scandium, and plutonium—all of which occur in only trace amounts in the biosphere, but have radioisotopes which are produced in significant quantities by man and accumulated by animals and plants. In the following discussions "metallic elements" will be used to refer generally to all of the elements mentioned above and in Table 1. Space will not permit separate discussion of each element; instead we will attempt to discuss those general aspects of ecosystem structure and function likely to be most significant in governing the flux of elements within and through estuaries and to identify those elements known to be valid examples or exceptions.

Although an estuarine ecosystem is very complex and difficult to model mathematically, we will take the approach of defining the variables which should be considered in a mathematical model of the dynamic cycling of metals in estuaries, with particular emphasis on the coastal plain estuaries of the southeastern United States.

MAJOR RESERVOIRS IN THE CYCLING OF ELEMENTS

In marine and estuarine environments, nearly all of any given metallic element occurs in the sediments and water (Duke, Willis, and Price, 1966; Duke et al., 1969; Pomeroy et al., 1969; Lowman, Rice, and Richards, 1971). Both sediment and water contain several individual reservoirs for elements, with some components much more important than others to cycling in the system. The "water components" include dissolved ionic forms, dissolved organic complexes, and suspended particulate matter—all of which interact with sediment compartments via adsorption, ion-exchange or sedimentation-resuspension processes. In tracer studies with ^{65}Zn, the rapid instantaneous uptake of radioisotope by estuarine sediments indicated a high rate of continuous exchange of zinc across the sediment-water interface (Duke, Willis, and Wolfe, 1968). In sedimentary deposits, elements may become "trapped" in deeper sediments and be effectively removed from further exchange with the system. In salt marsh, however, *Spartina* recycles phosphorus and zinc from deep subsurface sediments (Pomeroy et al., 1969), and burrowing animals such as crabs, polychaetes, and clams rework shallow and surface deposits, thereby prolonging contact with overlying waters (Gordon, 1966; Rhoads, 1967; Rhoads and Young, 1971). In preliminary studies on the exchange of zinc between estuarine sediments and water, the resuspension of sediments by the burrowing and feeding activity of polychaetes markedly increased the rate of loss of tracer ^{65}Zn from the water overlying the experimental cores (Duke et al., 1968, and unpublished observations). Surface silt layers of high organic content may be a major source of elements to deposit feeders in detritus-based food webs (Cross, Duke, and Willis, 1970; Lowman et al., 1966). In turbulent estuaries, these surface deposits may become suspended and be ingested by filter-feeding organisms such as menhaden, bivalve molluscs, and

zooplankton. Suspended particulate matter may arise also from the ultimate flocculation and precipitation of dissolved ionic species, such as Fe and Al, which are readily hydrated to form colloidal hydroxides at the pH of seawater (Riley and Chester, 1971). Other sources of suspended particulate matter include feces excreted directly into the water column by pelagic animals, cast-off exuviae from zooplankton, and dead planktonic organisms.

Different dissolved chemical species in the water undoubtedly represent discrete and significant reservoirs in the cycling of elements. Organic metallic complexes or chelates may equilibrate slowly with the ionic forms and have been shown or suggested to have drastically different availabilities to organisms. For example, EDTA (ethylenediaminetetraacetic acid) reduced the accumulation of ^{59}Fe by crabs (*Panopeus*), clams (*Mercenaria*), and oysters (*Crassostrea*) (Rice, 1965). Goldberg (1952) demonstrated that the marine diatom *Asterionella japonica* also could utilize iron if particulate or colloidal but not when complexed with citrate, ascorbate, or artificial humate. On the other hand, accumulation of cobalamin by clams (*Donax*) was much enhanced over accumulation of ionic cobalt (Lowman and Ting, in press); and it has been suggested that natural organic chelators may enhance the growth of phytoplankton (Barber and Ryther, 1969), thereby implying that organic complexes might constitute an important avenue for accumulation of metallic nutrients by marine organisms. Unfortunately, technology for the separation and identification of organic ligand-metal complexes from natural waters is in its early infancy, and one can only speculate on the significance of the various chemical forms present in estuarine waters. Regardless of the relative biological availabilities of metals from different organic complexes or from uncomplexed forms, the formation of soluble organic-metal complexes increases the holding capacity of estuarine water for a particular metallic element. Soluble organic complexes therefore probably decrease the net adsorption of metals onto sedimenting particulate materials, thereby increasing the metals' susceptibility to export via tidal flushing. The nonliving elemental reservoirs designated in Table 2 are thought to be of greatest significance in determining the distribution and flux of metallic elements in estuaries.

The estuarine biota consists of many species in a complex and interwoven network of feeding relationships. From a practical viewpoint, all species cannot be considered major elemental reservoirs for modeling purposes. One approach would be to group species by trophic position and consider each trophic level as a single reservoir. Many species, however, are opportunistic feeders with omnivorous habits which complicates their ready assignment to a particular trophic level and necessitates the use of fractional trophic levels. In addition, some species of comparable trophic position and abundances must be considered separately because one is desired as human food and another not. For example, oysters, clams, and scallops should be considered separately from other filter-feeding bivalve molluscs. Another example might be the primary carnivores, flounders and skates, of which only the flounder is harvested for human food. It is more feasible to group species wherever possible and consider individual species only where necessary. Preliminary surveys of the estuarine flora and fauna in the vicinity of Beaufort, N.C., suggest that the organisms in Table 2 should be considered as separate reservoirs or components. Some of the species are identified because of their commercial importance; others only because of their abundance and probable significance as forage. Organisms not identified to species have been lumped arbitrarily into "other" categories according to their feeding habits and trophic position.

The reservoirs identified in Table 2 as being "significant" or "important" in the cycling of elements in estuaries obviously are not all of equal importance. The list is probably incomplete, but at the same time may include some unnecessary designations. Most of the reservoirs identified to species have been considered in the development of a static model of annual energy flow in these estuaries (Williams and

Murdoch, 1970).[2] Quantification of the biomass in each of the major biological components is a primary objective of ecological research at the Atlantic Estuarine Fisheries Center, and preliminary estimates are currently available for the dominant macroorganisms (Williams, Thayer, Price, Kjelson, and Turner, Unpublished data). Analytical data on the concentrations of iron, manganese, zinc, and copper in these organisms and in sediments and water are also available or forthcoming (Cross et al., 1970; Cross and Brooks, in press; Wolfe, 1970a; Cross, Lewis, and Hardy[3]). Meaningful quantification of reservoir size for any element in certain components, however, will be extremely difficult to achieve (especially for the "other" categories, e.g., filter-feeding bivalves, deposit-feeding bivalves, carnivorous benthos, etc.). It may be practical to evaluate the importance of these "catch-all reservoirs" only by manipulating trial values for biomass and elemental concentrations during early phases of model development.

Pathways of elemental flux between reservoirs also are tentatively identified in Table 2. Individual transfer processes are designated in the matrix of Table 2 by an "I", indicating an influx of a metallic element from the reservoir at the top of the table to the reservoir on the left. Fluxes between biological reservoirs represent food chain transfers of elements. Such transfers usually involve one-way cyclic net flows (with internal loops) through the food web of the ecosystem. At this time the feeding habits of many of the listed species are incompletely known, and the food web of Table 2 must be regarded partly as the product of intuition and speculation.

The flux of elements between the organisms and the nonliving reservoirs is less readily identified, however, than the food web, because of uncertainty about the relative abundance and importance of different physical-chemical states, e.g., the ionic forms versus organic complexes. Physical-adsorption and ion-exchange processes, operative on biological (and nonbiological) surfaces, obviously would contribute to the total flux of an element; but since these processes are generally reversible, their importance to net transfers (especially at higher trophic levels) remains unknown. There must be a net influx of most elements from the soluble ionic phase to most organisms during their life span, however, simply because the surface area for adsorption increases during growth.

The significance of organic-metal complexes is unknown. We suspect that dissolved organic compounds constitute a mechanism for internal feedback loops involving all organisms at all trophic levels, except perhaps man. Thus, an organism may accumulate specific organic-metal complexes which undergo metabolic transformation, and the metals may in part be excreted as different organic complexes which reenter the cycle as nutrients for phytoplankton or heterotrophic microbes. We can only speculate now on whether there is net production or net utilization of metal-organic complexes by organisms. This ambiguity is indicated in Table 2 by a "double I" (i.e., by I's at both relevant intersects of the matrix), representing ingestion or absorption of organic-metal complexes by most organisms with simultaneous excretion of other organic complexes which might be quite different chemically.

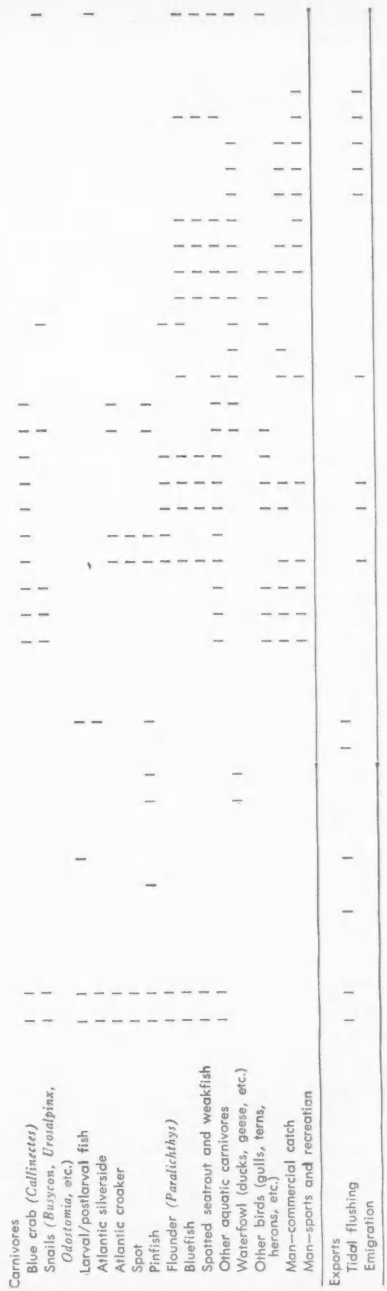
Fluxes between nonliving reservoirs are more dependent upon reversible physical processes, such as adsorption, ion-exchange, and sedimentation-resuspension. The net direction of flux may therefore depend on such variables as salinity, pH, and turbulence. The association of heterotrophic microbes with suspended particulate material probably results in a net influx of most metals into this reservoir from soluble sources with subsequent passage into detritus-based food chains. The extent of reversibility for the transfers (identified by "R" in Table 2) varies also from element to element. Thus, ^{137}Cs may be transported into estuaries on bed-load sediment and desorbed at higher salinities

[2] Williams, R. B., and M. B. Murdoch. 1970. A general evaluation of fishery production and trophic structure in estuaries near Beaufort, N.C. *In* Center for Estuarine and Menhaden Research Annual Report to the Atomic Energy Commission. Filed at NMFS Atlantic Estuarine Fisheries Center, Beaufort, N.C. 28516. [Processed.]

[3] Cross, F. A., J. M. Lewis, and L. H. Hardy. Concentrations of Mn, Fe, Cu, and Zn in four species of filter-feeding bivalve molluscs. Unpublished manuscript filed at NMFS Atlantic Estuarine Fisheries Center, Beaufort, N.C. 28516.

TABLE 2.—Major reservoirs and pathways of elemental flux in an estuarine ecosystem. I = influx from top to left; R = reversibility (see text)

	Soluble ionic	Soluble organic	Interstitial soluble	Subsurface sediments	Bed-load sediment	Surface sediment, detrital deposits and microflora	Suspended particulate, detritus and microflora	Salt grass	Benthic algae and epiphytes	Eelgrass and epiphytes	Phytoplankton	Zooplankton	Heterotrophic microbes	Meiofauna	American oyster	Hard clam	Bay scallop	Shrimp (*Penaeus*)	Shrimp (*Palaemonetes*)	Atlantic menhaden	Striped mullet	Bay anchovy	Other filter feeders	Other deposit feeders	Blue crabs	Snails	Larval/postlarval fish	Atlantic silverside	Atlantic croaker	Spot	Pinfish	Flounder	Bluefish	Spotted seatrout and weakfish	Other carnivores	Water fowl	Other birds	Import from watershed or precipitation or human effluents	Import via immigration
Nonliving reservoirs																																						
Soluble ionic													I																									
Soluble organic	R																																				
Interstitial soluble	R	R				I			I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Subsurface sediments			R																																		
Bed-load sediment	R		R			I																															
Surface sediment, detrital deposits and microflora	R	R	R		R				I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Suspended particulate, detritus and microflora	R	R			R	R			I	I	I	I	I																								
Primary producers																																					
Salt grass (*Spartina*)	I	I	I																																		
Benthic algae and epiphytes	I	I																																			
Eelgrass and epiphytes	I	I			I		I																														
Phytoplankton	I	I																																			
Herbivores																																					
Zooplankton	I	I									I																										
Heterotrophic microbes	I	I				I					I			I		I																					
Meiofauna	I	I	I			I																															
American oyster (*Crassostrea*)	I	I								I																											
Hard clam (*Mercenaria*)	I	I								I																											
Bay scallop (*Argopecten*)	I	I								I																											
Shrimp (*Penaeus*)	I	I				I				I																											
Shrimp (*Palaemonetes*)	I	I				I																															
Atlantic menhaden	I	I								I	I																										
Striped mullet	I	I				I				I	I		I																								
Bay anchovy	I	I								I	I																										
Other filter feeders	I	I	I							I																											
Other deposit feeders	I	I	I			I				I			I																								
Blue crabs																																					
Snails																																					
Larval/postlarval fish																																					
Atlantic silverside																																					
Atlantic croaker																																					
Spot																																					
Pinfish																																					
Flounder																																					
Bluefish																																					
Spotted seatrout and weakfish																																					
Other carnivores																																					
Water fowl																																					
Other birds																																					
Import from watershed or precipitation or human effluents																																					
Import via immigration																																					



(Wolfe, 1971); whereas ^{65}Zn may be irreversibly adsorbed onto estuarine sediments (Johnson, Cutshall, and Osterberg, 1967). The actual flux of any given element through the complex interwoven network of pathways tentatively identified in Table 2 is in a state of dynamic equilibrium affected by system imports and exports and by a number of environmental variables, to be discussed in the following sections.

INPUTS AND OUTPUTS OF ELEMENTS TO AND FROM ESTUARIES

System inputs and outputs consist of the physical translocation of elemental reservoirs (sediment, water, and biotic components) across the boundaries of the estuarine system (Table 2), and fluxes of other materials (nonreservoirs) which influence the distribution or movement of elements among the system reservoirs. Rainfall is a dominating system input, which introduces small amounts of some elements directly as aerosols (Gorham, 1961), but exerts its greatest influence in the form of runoff. The volume and flow rate of runoff in turn determine the amount and composition of elements leached from the land and the size of the bed load of eroded sediment transported into the estuary. The volume and flow of runoff also interact with the tidal volume to affect the flushing rate for the estuary. Tidal flushing continuously removes from the estuary a fraction of the dissolved and suspended materials, including the planktonic reservoirs. The tidal volume also represents an input of ocean water, but since seawater contains less of most metallic elements than estuarine waters, net loss from the estuary probably results. If, on the other hand, the coastal or estuarine waters contained an excess of uncomplexed organic material, seawater might represent an input of soluble ionic metallic elements which could accumulate in the estuary through sedimentation, or be removed from the estuary as organic complexes, either by flushing or bioaccumulation.

Variable wind speed and direction affect water circulation patterns particularly in shallow estuaries and thereby vary the "normal" flushing characteristics of an estuary. Circulation within

the estuary obviously determines also the physical distribution of certain reservoirs within the system, and this aspect of cycling compounds the difficulties of developing a realistic model. Application of the term "ecosystem" to an estuary, however, implies that an estuary behaves as a discrete, identifiable unit and, despite the clumped distributional patterns exhibited by organisms in the environment, spatial distribution of reservoirs within the system is assumed insignificant; i.e., the system model is homogeneous.

In addition to tidal flushing of planktonic organisms, biotic inputs and outputs include the contribution of terrestrial primary productivity, brought into estuaries as dissolved organic material and particulate organic detritus in runoff, and the seasonal migrations of larger invertebrates and fish into and from estuarine waters.

A final input which must be considered consists of human waste materials. Organic waste materials affect productivity and biological species structure of the ecosystem and probably also affect the availability of metallic elements through organic complexing. In addition, large amounts of certain metallic elements are introduced into many estuaries directly in industrial and municipal effluents.

FACTORS INFLUENCING DISTRIBUTIONS AND TRANSFERS OF ELEMENTS AMONG THE VARIOUS RESERVOIRS IN ESTUARIES

The various groups of biota, the dissolved and particulate components in the water column, and sediment compartments, represent the major reservoirs per se for metallic elements, but the interaction of these compartments and regulation of their sizes are influenced greatly by other variable characteristics or components of estuarine ecosystems including inputs of energy and auxiliary materials or factors which affect reservoir sizes or transfer rates within the system. These factors represent "nondynamic state variables" in the modeling terminology of Kowal (1971). These characteristics may be categorized as: (1) those that affect productivity in the trophic web and (2) those that affect the physical state or rates of exchange between components for the specific elements of interest. The influences of major nondynamic state variables are summarized briefly in Table 3.

Solar energy is perhaps the best example of the first type of input. Solar energy drives the primary productivity supporting all the biotic reservoirs and establishes the basic temperature regime for the entire system, which is a dominant factor influencing the rate of material transfer processes, biological and nonbiological. The seasonal variability of temperature can readily be incorporated into systems models according to a sinusoidal function. This general approach has been described and applied by Williams (1969). In the first category also are dissolved gases, e.g., CO_2 and O_2, and inorganic nutrients, especially the various forms of P and N. Certain dissolved organics may also be included here, although absolute requirements for these have not been demonstrated in the nutrition of estuarine organisms, and dissolved organic-metal complexes constitute a major reservoir already considered. Acidity, or pH, is an important factor in that it acts with temperature to control CO_2 solubility and thereby affects primary productivity, but pH also falls into the second category because it determines the equilibrium distribution of metals in adsorption reactions, i.e., exchange between water and sediments, or between water and biological surfaces; and in chelation reactions, including metal-organic complexes in the dissolved phase.

Wind is another significant energy input in shallow estuaries. Wind increases turbulence and suspension of particulate matter which promotes exchange of elements between water and sediments and affects the size of the suspended particulate reservoir subject to flushing.

Salinity is also a determinant in the distribution and cycling of elements. Salinity, as a measure of ionic strength, affects the adsorption equilibria established between sediments and water and biological surfaces and water, and probably also influences the configuration of proteins and other biological polymers which form complexes with metals. This mechanism may be the basis of salinity effects on active transport processes in ionic and osmotic regulation in es-

TABLE 3.—Role of nondynamic state variables.

Factor	Compartment and sign (+ or −) of correlation	
Fe, Al, Mn, etc.	Suspended particulate	+
Nutrients (nitrate, nitrite, ammonia, phosphate, and silicate)	All primary producers and microbial heterotrophs	+
Solar insolation	All primary producers	+
Temperature	Exchange rates	+
	Adsorption	−
	Respiration	+
Season of year	Inputs and outputs via migrations	±
Wind speed and wind direction	Suspended particulate	+
	Flushing export rate	±
Dissolved carbon dioxide	All primary producers	+
Dissolved oxygen	Respiration	+
pH	Surface adsorption	+
Salinity	Surface adsorption	−
	Ion-exchange rates	+
Precipitation	Inputs of sediment bed-load	+
	Suspended particulate	+
	Dissolved ionic	+
	Dissolved organic	+

tuarine organisms. In addition, salinity provides a measure of bulk components of seawater, e.g., Ca and K, which may compete directly with trace components for adsorption sites of biological accumulation, e.g., Sr and Cs. For example, increasing salinity decreases the accumulation rate and concentration factor for ^{137}Cs in estuarine clams (Wolfe and Coburn, 1970). Salinity is correlated also with the concentration of ^{137}Cs in lower-salinity estuarine water, possibly as a result of mass action on the sediment-water exchange equilibrium (Wolfe, 1971). Important dissolved trace components include Fe, Al, and Mn, whose concentrations depend less on salinity than on watershed characteristics and runoff. At the pH, Eh, and ionic strength characteristic of seawater, these elements form insoluble hydroxides which flocculate and provide adsorptive surfaces for other elements. Such a coprecipitation process may be an important determinant in the distribution of fallout ^{106}Ru in estuaries (Wolfe and Jennings, in press).

For any given estuary the chemical environment and flushing characteristics are affected greatly by the geological and chemical characteristics of the watershed area, the type of estuary (stratified vs. well-mixed, etc.), and the physical size, shape, and orientation of the estuarine basin. Such characteristics must be considered when different estuaries are compared.

A set of biological processes accompanies each trophic interaction and determines the efficiencies for transfers of biomass between components. These are feeding or ingestion rate, digestion rate, assimilation efficiency, respiration, and growth efficiency. Each of these characteristics may be influenced in turn by various environmental factors, such as temperature and salinity (Peters and Boyd, in press; Peters and Angelovic, in press).

Assimilation and respiration maintain the biomass of the biological reservoirs for elements, but the accumulation and retention of most metallic elements are probably not directly correlated with the assimilation and respiration of carbon. For dynamic modeling of the cycling of metallic elements in the estuarine biota, however, it is essential to consider the changes in biomass as well as changes in concentration of the element of interest. The interrelation of ^{65}Zn-excretion and respiration has been examined directly for pinfish, *Lagodon rhomboides*, (Hoss, 1971). Lowman et al. (1971) computed assimilation efficiencies ("conversion factors") for the transfer of several metallic elements from oceanic phytoplankton to zooplankton, based upon

relative concentration factors in zoo- and phytoplankton and a mean carbon assimilation of 50%. On this basis, assimilations for 24 elements ranged from 1 to 85%—indicating nonparallelism with carbon assimilation—but Lowman went on to say: "The major weakness in this method of calculating conversion factors for a variety of elements is the uncertainty of the accuracy of the concentration factors for phytoplankton and zooplankton." Similar uncertainty exists for published concentration factors for various elements in estuarine organisms, especially since environmental conditions (and therefore elemental concentrations in estuarine water) are subject to such wide variation. A further complication is the uncertainty concerning the proportion of total elemental intake represented by food sources. According to Polikarpov (1966), marine animals satisfy their requirements for most elements by direct absorption from the surrounding water. Considerable experimental evidence, however, supports the importance of food as a source of elements for many organisms (Rice, 1963; Hoss, 1964; Baptist and Lewis, 1969). Atoms adsorbed directly from the water onto body surfaces, whether internal or external, do contribute to the concentration factor but have no relevance to assimilation of food. Surface adsorption frequently results in assimilation, however, as in phytoplankton (Goldberg, 1952) and the mantle epithelium of Pelecypoda (Nakahara and Bevelander, 1967). For organisms with well-defined and easily analyzed internal tissues, e.g., crustacean and fish muscle, internal concentrations of elements probably represent the assimilated fraction, but for many smaller or less differentiated organisms, internal tissues cannot readily be separated from adsorptive surfaces. Assimilation efficiency may depend also on biochemical composition of the food —at least at certain trophic levels. For example, the assimilation of ^{65}Zn by human subjects was 35% from a diet of whitefish (Honstead and Brady, 1967) and 13.5% from oysters (Honstead and Hildebrandt, 1967), showing a high (though perhaps coincidental) positive correlation with the protein content of the foodstuff (Wolfe and Rice, 1968).

The concentration of an element in representatives of a population of organisms is a function of the turnover time for the element and the average life span of the organism. Long-lived organisms probably achieve a steady state for the turnover of most elements after the cessation of growth—and if the availability of the element from the organism's environment is stable. In organisms with rapid growth and high population turnover, net accumulation probably proceeds for most metallic elements throughout the entire short life span of the organism, and steady state is not reached before the organism is consumed by the next trophic level. The environmental and physiological factors determining the steady state conditions are not known, however. Many organisms may accumulate metallic elements far in excess of their biological requirements (Wolfe, 1970b; Pequegnat, Fowler, and Small, 1969), and accumulation of metals may continue independent of the biological necessity in some cases until available reaction sites (e.g., between metal and proteins or tissue surfaces) are saturated. This process is suggested also by the increasing concentration of mercury with age (or size) in various fish (Westö, 1969; Bache, Gutenmann, and Lisk, 1971).

In a dynamic estuarine system, where environmental levels of metallic elements are subject to rapid fluctuations, the organismic response to environmental change must be identified. Information of this nature is sorely lacking in the literature. Pringle et al. (1968) tested the response of oysters to various increased experimental levels of lead, and after 49 days exposure, accumulation had proceeded in direct relation to availability of lead in the environment. Other data (Chipman, Rice, and Price, 1958; Preston, 1967; Wolfe, 1970a) suggest that concentration factors for Zn in oysters are inversely related to zinc content of water, implying that net accumulation would diminish or cease at some high environmental concentration (low concentration factor in oyster) and steady state would be established. In these cases, however, the variability of instantaneous uptake of the element can only be inferred from the amounts contained after a long period of accumulation. In natural ecosystems, fallout radioisotopes appear in estuarine organisms very quickly after initial entry of the

isotopes into the ecosystem (Wolfe and Schelske, 1969; Wolfe and Jennings, in press). A high rate of instantaneous uptake has also been demonstrated for many organisms and many elements in experiments on radioisotope accumulation, but, in most cases, concentrations of stable element counterparts for the radioisotopes were undetermined so that rates of flux for the stable element could not be computed from the observed flux of radioactivity. Although the accumulation and turnover of a radioisotope in a single component can be modeled mathematically independent of the stable element chemistry (Reichle, Dunaway, and Nelson, 1970), it is the flux of stable elements which determines the movement of radionuclides among the various components of an ecosystem and investigators should routinely collect data on the stable element composition of the compartments involved in their accumulation studies. In this way, experimentally observed radioisotopic accumulation rates can be used in conjunction with the specific activity, i.e., the concentration ratio of radioisotope to total element, to determine rates of elemental turnover. It seems probable that instantaneous uptake of an element is a direct function of available environmental levels whereas instantaneous loss is a direct function of accumulated amounts. The instantaneous uptake rate is also a function of other environmental variables. For example, in the estuarine clam *Rangia cuneata*, the instantaneous uptake rate and the equilibrium concentration of ^{137}Cs increase with temperature and decrease with salinity (Wolfe and Coburn, 1970). Salinity, temperature, pH, and total Zn also influenced the accumulation of ^{65}Zn by various estuarine organisms under experimental conditions (Duke et al., 1969).

Net accumulation (or net loss) results when instantaneous uptake exceeds (or is less than) instantaneous loss, and the physiology and metabolism of the organism determine the residence times required for passage through its many alternate internal compartments and pathways. Retention times are usually discussed in terms of biological half-life. (See for example Baptist, Hoss, and Lewis, 1970.) Since organisms have several compartments simultaneously interacting with the environment, retention typically consists of several components with different rates. One might expect the faster rates to be associated with surface adsorption reactions, intermediate rates with excretion of unassimilated material as feces, and slow rates with the turnover of the assimilated and metabolized fraction of the elemental content. Although the relative amounts of an accumulated radioisotope involved with different retention components can be determined for the particular conditions and time period of accumulation and loss used in the experiment, these amounts will not be representative of stable element pools unless all of the internal compartments are equally labeled, i.e., to a uniform specific activity. Thus, long-term accumulation experiments under conditions of constant specific activity are required (Cross, Willis, and Baptist, 1971). The individual retention components for an element probably will have to be considered for each important reservoir in modeling the overall flux of that element in the ecosystem.

We have discussed several aspects of elemental cycling in estuaries and have demonstrated the incompleteness of man's knowledge of how an estuary operates as a system with many integral, smoothly functioning components. We believe, however, that many of the unsolved problems which have presented themselves will be realistically resolved only by a holistic approach to ecological research. The foregoing discussion represents an effort to conceptualize the elemental cycling system that operates in our southeastern coastal zone estuaries. Prior recognition of the complexity and integrity of the system as a whole provides an improved basis for planning meaningful research on the transfer processes between individual components of an estuary. Considerable research is required before we can actually quantify the reservoirs, routes, and rates of elemental flux involved in this preliminary model of these ecosystems. The complexity of the ecosystem defies precise quantification of all the reservoirs and all the transfer rates under any set of environmental conditions. In such a system, however, the predictability of the magnitude and variability of any elemental reservoir depends upon recognition of all the interactions impinging upon that reservoir. Research now

in progress at the Atlantic Estuarine Fisheries Center will enable us to estimate the size ranges for most reservoirs of manganese, iron, and zinc in our local estuarine system. The major gaps in our present knowledge lie in:

1. Determining the relative amounts of different physico-chemical forms of an element or radioisotope in natural waters, their relative stabilities, and the ease of interconversion between the various forms.

2. Determining the relative biological availabilities of these different physico-chemical forms to various types of biota.

3. Determining trophic structure of the entire ecosystem. The role of microorganisms—as sources of metallic elements to consumers in detritus-based food chains, as producers of organic-metal complexes, and as remineralizers of metals previously incorporated into plant or animal tissues—is particularly poorly understood.

4. Determining feeding rates and assimilation efficiencies for carbon and metallic elements at each major trophic interaction.

5. Determining biological retention of metallic elements in the major organisms consumed by man.

6. Determining the interactions of variable environmental parameters on reservoir size and transfer rates at each step in the overall system.

As further information becomes available, this preliminary systems model will be refined and tested as to its adequacy for describing the flux of manganese, iron, and zinc in our local estuarine system. Maintenance of this sort of holistic viewpoint toward ecological function and continuous updating of existing conceptual models will provide the most reliable basis for rational management of man's releases of toxic heavy metals and radionuclides—or indeed, of any contaminant additions to the environment.

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A LABORATORY STUDY OF PARTICULATE AND FILTER FEEDING OF THE PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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ABSTRACT

In laboratory feeding trials Pacific mackerel, *Scomber japonicus*, averaging 147 g in weight did not respond to *Artemia* nauplii, but did capture *Artemia* adults by biting (particulate feeding) when density was 1 or 2/liter and by filtering when density was 22 to 112/liter. Particulate feeding is described by $N_P = 60.3tD$, where N is the number of *Artemia* ingested in t minutes at D numbers per liter. Filter feeding is described by $N_F = 23{,}788\ (1 - e^{-0.0036tVD})$, where 23,788 is an asymptotic estimate of the number of *Artemia* in the digestive tract at full capacity.

The results suggest that the mackerel utilizes only the larger of the planktonic crustaceans, such as euphausiids, in the sea. For the relatively low average densities of such organisms the derived equations indicate that the mackerel could not obtain its daily nutritional requirement, estimated to be 8% of body weight, in less than 24 hr of feeding. Though the daily requirement could be obtained in much shorter periods, perhaps by filter feeding, if such crustaceans are encountered in aggregations of considerably higher density than reflected by area averages, it is probable that the mackerel must often depend in part on such larger organisms as fish to fulfill its needs.

Comparison of the mackerel ingestion rates to those for the smaller northern anchovy indicates that while the individual mackerel may generally capture a greater proportion of the large crustaceans encountered than the anchovy, the proportion captured would have a relatively lower nutritional value for the mackerel.

The Pacific mackerel, *Scomber japonicus*, is one of several pelagic schooling fishes of the eastern temperate Pacific which feed on zooplankton, but it does not depend entirely on zooplankton. Fitch (1956) reported that stomach contents contained about 30% larval and juvenile fish by volume, with the remainder composed largely of such crustaceans as mysids, copepods, and euphausiids. Frey (1971) commented that larval and juvenile fish appear to be the most important food, but that the mackerel relies heavily on euphausiids at times. Hatanaka et al. (1957) showed that *S. japonicus* in coastal regions of Japan consume mainly small anchovies in the late summer and autumn and euphausiids in other seasons. The biomass of euphausiids consumed annually was estimated to be three or four times that of anchovies.

In addition to being the dominant element in the diet of *S. japonicus*, the larger crustaceans are an important class of food for a number of other pelagic schooling fishes. The jack mackerel (*Trachurus symmetricus*) is known to feed heavily on small fish and squid at times (Fitch, 1965), but about 70% of stomach contents by volume is euphausiids (Carlisle, 1971). The Pacific sardine (*Sardinops caerulea*) feeds largely on copepods smaller than those consumed by the jack mackerel but is occasionally gorged on euphausiids, and these average about 5% of stomach contents by volume (Carlisle, 1971). The northern anchovy (*Engraulis mordax*) consumes phytoplankters and small zooplankters, but large copepods and euphausiids appear to be the most important food items (Loukashkin, 1970). Thus while all of these species prey on

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large crustaceans, the latter do not necessarily make an equivalent contribution to their diets. It is probable that the segment of the biota represented by such crustaceans in the sea is a food source of different potential for different fishes.

Assessing the food potential of large crustaceans for the Pacific mackerel, or any of the above teleosts, requires a knowledge of the density levels of such crustaceans in the sea and of the rates at which the organisms can be captured in relation to density. Leong and O'Connell (1969) determined by a laboratory study the rates at which the northern anchovy feeds on *Artemia* nauplii by filtering and on *Artemia* adults by biting (particulate feeding), and O'Connell (1972) showed that the two kinds of feeding activity in a small school varied with the relative abundance of the two sizes of *Artemia*. The present study was undertaken to obtain comparable information for the Pacific mackerel, using *Artemia* as the food. The results are discussed in respect to the densities of large crustaceans in the sea and in respect to the feeding rates of the anchovy.

METHODS

Feeding trials were carried out in an arrangement of two plastic pools with a connecting trough and gates (Leong and O'Connell, 1969; O'Connell, 1972). The pools were supplied with a continuous flow of filtered sea water and each contained 4.5 m^3 of water at a depth of 0.61 m (2 ft). They were under a 12-hr day, 12-hr night cycle of illumination, but all trials were carried out during the day. Temperature varied from 16° to 19°C.

A school of about 160 mackerel was acclimatized in the pool arrangement with the gates open for about 2 weeks and then confined to one pool before the study started. The fish averaged 222 mm (202 to 247 mm) in standard length and 152 g (100 to 225 g) in weight. The latter average is based on weights taken at the end of each feeding trial and included digestive tract contents, which were later found to range from 0.1 to 21.8 g. These values were subtracted from the measured fish weights to obtain estimates of the weights before feeding. The subsequent analysis involves the adjusted weights, which averaged 147.3 g.

All feeding trials were preceded by at least 24 hr without feeding, which was enough to produce virtually empty digestive tracts in preliminary investigations. For each trial the water flow was turned off, and four fish were diverted from the holding pool to the trough and then admitted to the prepared food situation in the other pool where they were allowed to feed for a given number of minutes. Closing of the gate after admission initiated the time period and introduction of a hinged crowder, which was rapidly closed to trap and remove the fish, terminated the time period. The fish were killed in less than 2 min after introduction of the crowder, immediately measured and weighed, then placed in jars of 10% Formalin with the body cavity opened.

Though the study is concerned primarily with feeding on *Artemia* adults, a few feeding trials were carried out with newly hatched *Artemia* nauplii, which averaged 0.65 mm in length, to document the response of the mackerel to very small crustaceans. The densities in the water were estimated from subsamples, and quantities in the digestive tracts were estimated by total counts or volumetric aliquoting, as described by Leong and O'Connell (1969).

Feeding on *Artemia* adults is based on digestive tract contents of four fish in each of 28 trials, with each trial representing a different combination of food density and feeding time (Table 1). The food situation was established for each trial by placing a given wet weight of *Artemia* adults in the experimental pool and dispersing it gently with wide-mesh dip nets just before admitting the fish. The weights given under food quantity are the wet weights introduced at the start of each trial. These were selected after preliminary observation to include the highest and the lowest levels that could be managed conveniently. The multiplication factors given in certain cells of the table indicate the number of times the specified weight was introduced into the pool during the trial, e.g., 20 g was introduced six times, or at 15-min intervals, during the 90-min trial. This was done to sustain the nominal food den-

TABLE 1.—The array of trials with respect to food density and feeding duration. Number/liter is the nominal density for the weight introduced.

Quantity of *Artemia*		Minutes of feeding					
Total weight	Number liter	2.5	5	10	30	60	90
g							
10	1	1	1	1	1(3×)[1]	1(6×)	1(9×)
20	2	1	1	1	1(2×)	1(4×)	1(6×)
200	22	1	1	1	1	1	1
590	66	1	1	1	1	1	1
1,010	112	1	1	1	1	--	--

[1] The multiplication factors show the number of times, at equal intervals, that the specified weight was introduced during the trial to maintain the nominal density. See text.

sity over long periods at the lower food density levels. Introduction of food during the trial, and even brief dispersion with the wide-mesh net, did not appear to distress the fish and scarcely interrupted their feeding activity.

The intervals of food introduction for the lower density levels were determined from a preliminary study. During a 30-min trial with 20 g of *Artemia*, e.g., feeding activity declined sharply after 15 min, and average digestive tract contents did not differ from that for a trial of 15 min. A trial of 30 min with two introductions of 20 g showed approximately double the digestive tract contents of the above two. The 10-min interval for 10 g introductions was established from similar considerations. Food availability remained high throughout the trials at the three higher density levels.

The nominal densities of *Artemia* shown in Table 1 are based on the volume of the pool and a conversion factor of 500 *Artemia* adults/g wet weight. The conversion factor is an average derived from samples from the several batches of *Artemia* delivered to the aquarium. Portions of these samples also indicated that individuals averaged 4.5 mm in length and 0.48 mg dry weight.

The quantities of *Artemia* in the digestive tracts of the fish were estimated separately for the mouth, the esophagus and stomach combined, and the anterior and posterior halves of the intestine. The contents of the esophagus and stomach were weighed. Numbers in the various sections were estimated by total count where quantity was low, but by counts from aliquots where the quantity was large. These data indicated that the weight of ingested *Artemia*, determined 2 to 6 months after preservation, was 25 to 50% lower than the weight of the live organisms. Digestion and leaching by Formalin may have been responsible for such loss. Since the weights of food in the digestive tracts could not be considered representative of the weights of food consumed, the analysis was carried out on the numbers of organisms in digestive tracts.

Values for all sections of the digestive tract were pooled to obtain estimates of total digestive tract contents, the primary entity in analysis. The numbers found in the mouth varied from less than 1 to 53% and averaged 18% of total digestive tract contents. This percentage, furthermore, varied with food density, increasing from 4% at the 10 g level to 41% at the 1,010 g level. It is presumed that the contents of the mouth were accumulations to be swallowed and/or material regurgitated during capture. Proportions in the intestine were considerably lower and will be described later.

RESULTS

RESPONSE TO *ARTEMIA* NAUPLII

Three trials were carried out with newly hatched *Artemia* nauplii as the only available food. In two cases the average densities of nauplii were about 190/liter and 230/liter, and groups of four fish showed no recognizable feeding activity during 30-min periods of exposure. In the third case density was a little more than 200/liter and a group of approximately 50 fish showed no feeding activity. The stomachs of five fish from these trials contained no nauplii, although a few nauplii were found on the gill rakers of two of them.

One trial was carried out with *Artemia* adults and nauplii both present in the water. The density of adults was 22/liter and the density of nauplii was 185/liter. After feeding for 5 min, four fish averaged 2,334 *Artemia* adults and 823 *Artemia* nauplii (635 to 1,083) in the mouth, stomach, and esophagus combined. The bulk of both sizes of organism was in the stomachs.

From these results it is evident that while the Pacific mackerel did not respond to nauplii alone,

it did ingest them along with the larger *Artemia* when both were present in the water. However, the dry weight of the nauplii ingested would be about 0.1% of the dry weight of the adults ingested. It appears, also, that the uptake of nauplii was only about 4% as efficient as the uptake of adult *Artemia*, i.e., the number of nauplii per fish represents 4.4 liters of water in the pool, while the number of adults per fish represents 106 liters.

Yasuda (1963) obtained results comparable to the above for *S. japonicus* 120 to 130 mm in length. He found that the mackerel did not eat brine shrimp (0.38 mm in length and presumably nauplii) as did anchovies (*Engraulis japonica*) and even horse mackerel (*Trachurus japonicus*) of approximately the same length. The spacing between gill rakers and gill raker processes was shown to be smaller in the latter two species than in the Pacific mackerel.

RESPONSE TO *ARTEMIA* ADULTS

The 28 trials in which *Artemia* adults were the only available food showed that feeding was particulate at the two lower density levels and filtering at the three higher density levels. Particulate feeding is the capture of individual organisms by directed biting. Filter feeding is the process of straining organisms from the water as it passes through the gill rakers while the mouth remains open. The duration of mouth opening was 1 to 3 sec, and such mouth openings occurred almost rhythmically 15 to 20 times/min. Filtering, however, was sustained for only a limited time, and this time varied inversely with density level of the food. It lasted 30 min at 22 *Artemia*/liter, 20 min at 66 *Artemia*/liter, and about 15 min at 112 *Artemia*/liter. At these times the fish noticeably reduced swimming speed and shifted to particulate feeding. Though particulate feeding appeared to be less vigorous under these circumstances than at the two lowest food densities, complete cessation of feeding did not occur in any of the trials.

The trial groups of four fish evidenced some discomfort upon encountering the highest food density, 112 *Artemia*/liter. Swimming speed and coloration showed less increase than at other densities, and filtering intervals were shorter and less rhythmic. A school of about 70 fish introduced to this highest density, on the other hand, exhibited strong rhythmic filtering accompanied by marked intensification of color and increased swimming speed. Though digestive tract contents from the fish of this group were not significantly greater than for the four-fish group after 5 min of feeding, the larger group virtually eliminated the available food in this time while the smaller group did not noticeably affect its density.

Preliminary analysis indicated that there was no confounding of size of fish with density levels and suggested that the larger fish tended to consume slightly more food at all densities. Hence, estimates of total digestive tract quantities were standardized to the average adjusted weight of all fish (147.3 g) by simple proportion. The means and standard errors of the standardized numbers are shown for each trial in Table 2. The greatest change in a trial average resulting from standardization was 20% of the original estimate, and the change was 5% or less for half of the trials. Standardization also affected the estimates of variability, but only to the extent that the coefficients of variation averaged 1% higher.

A separate analysis for each of the food density levels indicated that digestive tract contents increased proportionately with time at the two lower densities, but increased exponentially toward an asymptotic value at the three higher densities. It was also evident that the density-specific rates of increase varied directly with density for the two lower levels and with the square root of density for the three higher levels. The modes of food accumulation for the two density ranges can therefore be expressed as

$$N_P = \alpha t D \qquad (1)$$

and

$$N_F = N_\infty \left(1 - e^{-\beta t \sqrt{D}}\right) \qquad (2)$$

where N_P = number of organisms in the digestive tract after t minutes of particulate feeding,

TABLE 2.—The average fish weight and the mean ($\bar{X}$) and standard error (SE) of the standardized number of *Artemia* in the digestive tract for each trial.

Density	Feeding duration	Number fish	Average fish weight	Number in digestive tract	
Number/liter				$\bar{X}$	SE
	min		g		
1	2.5	4	125	149	60
	5	4	130	299	168
	10	4	136	572	86
	30	4	134	2,280	373
	60	3	135	3,430	342
	90	4	150	5,620	216
2	2.5	4	149	254	37
	5	4	148	695	81
	10	3	149	1,530	163
	30	4	123	4,636	583
	60	4	157	5,790	684
	90	4	149	11,325	1,204
22	2.5	2	136	745	263
	5	4	159	2,013	101
	10	3	141	4,399	270
	30	3	135	10,893	790
	60	4	165	15,664	648
	90	4	152	18,079	1,143
66	2.5	3	159	1,502	197
	5	3	139	4,041	409
	10	4	158	5,232	858
	30	4	174	9,863	990
	60	4	158	12,676	484
	90	4	168	15,723	605
112	2.5	3	145	3,079	936
	5	3	155	3,617	447
	10	4	139	7,629	982
	30	4	147	15,845	2,600

N_F = number of organisms in the digestive tract after t minutes of filter feeding,

D = the nominal density of food in numbers per liter,

N_∞ = asymptotic number of organisms in the digestive tract at full capacity,

α = specific feeding rate, and

β = instantaneous feeding rate.

Fitting all of the data in the two low density series with equation (1) and those in the three high density series with equation (2) resulted in a satisfactory fit for the low density group but not for the high density group. Calculated values tended to be lower than trial values for the 22 *Artemia*/liter series, and higher than trial values for the 66 *Artemia*/liter series, particularly for the longer time periods. The difficulty arises from the fact that average quantities in the digestive tracts were lower for the 66 *Artemia*/liter level than for the 22 *Artemia*/liter level in the 30-, 60-, and 90-min trials. The reason for this is not known, but examination of the quantities in the anterior and posterior halves of the intestine for all trials (Table 3) offers a plausible explanation.

TABLE 3.—Average number of *Artemia* in anterior (A) and posterior (P) halves of intestine for each trial.

Time		Density				
		1	2	22	66	112
2.5	A	0	15	9	33	300
	P	0	0	0	0	0
5.0	A	0.3	15	108	101	175
	P	0	0	0	0	0
10	A	1.8	50	57	215	467
	P	0	0	0	10	59
30	A	50	51	320	1,077	1,265
	P	0	0	36	327	245
60	A	0.7	165	830	569	
	P	0	45	720	714	
90	A	141	209	890	937	
	P	4	339	385	722	

At 22 *Artemia*/liter the maximum quantity in the intestine is reached at 60 min, and at 66 *Artemia*/liter the maximum is reached at 30 min. Fluctuations in the two halves of the intestine thereafter suggest posterior movement of material and intermittent elimination. This is corroborated by visual observations made during the trials. The earliest detected defecations were at 50 min for the 22 *Artemia*/liter level and at about 30 min for the 66 *Artemia*/liter level. No defecation was detected in the trials at 112 *Artemia*/liter, which did not go beyond 30 min. The quantities in the intestine suggest that rate of movement of material into the posterior part of the intestine approached the maximum at 66 *Artemia*/liter and that defecation might not start any sooner at 112 *Artemia*/liter than at 66 *Artemia*/liter.

From these data it is reasonable to suppose that beyond 30 min the time-specific losses by defecation would be greater for the 66 *Artemia*/liter series than for the 22 *Artemia*/liter series, and negligible for the two lower density levels.

On the supposition that the greatest underestimates of total amounts consumed occurred in the three longest time periods of the 66 *Artemia*/liter series, equation (3) was refitted to

TABLE 4.—Estimated parameter values and 95% confidence limits for density series separately and pooled under particulate and filter feeding.

	Particulate feeding	
Artemia/liter	Intercept	Slope (α)
1	46.8 (−316; 410)	61.5 (53.5; 69.5)
2	181.3 (−1,004; 1,367)	58.5 (45.9; 71.1)
Pooled	0 assumed	60.3 (56.3; 64.3)
	Filter feeding	
Artemia/liter	Asymptote (N_∞)	Instantaneous feeding rate (β)
22	20,322 (16,736; 23,908)	0.0052 (0.0031; 0.0074)
66	15,384 (13,991; 16,778)	0.0045 (0.0035; 0.0060)
112	22,050 (16,999; 27,102)	0.0040 (0.0029; 0.0059)
Pooled[1]	23,788 (21,802; 25,775)	0.0036 (0.0032; 0.0042)

[1] The pooled array under filter feeding does not include the 30-, 60-, and 90-min trials for 66 *Artemia*/liter.

the data for the higher density levels with these three trials removed. The estimated parameters are shown, along with those for the lower density levels, and also for the density levels individually, in Table 4. Since the individual series under particulate feeding did not have intercepts that differed from zero, the parameters for the pooled array were estimated with the intercept assumed to be zero. Goodness of fit for the combined data in both density groups was judged satisfactory; in Figure 1 the calculated curves are compared to the standardized trial means and standard errors for each density series. The equations for the two feeding modes can be stated as

$$N_P = 60.3tD \quad (3)$$

and

$$N_F = 23{,}788\left(1 - e^{-0.0036t\sqrt{D}}\right) \quad (4)$$

The asymptotic level, 23,788 *Artemia*, is indicative of the maximum capacity of mackerels at an average weight of 147 g. On the basis of the wet weight of *Artemia*, 500 individuals/g, maximum capacity would be 48 g, or 32% of fish weight. This is about double the greatest weight of fish food removed from the esophagus and stomach, but the two kinds of estimate are not necessarily inconsistent. As suggested earlier, the weights of the digestive tract contents may have underestimated the weights of *Artemia* in the live state by 25 to 50% because of digestion and leaching in Formalin. The estimate given here is based on weight of live organisms. Since digestion is going on during protracted feeding,

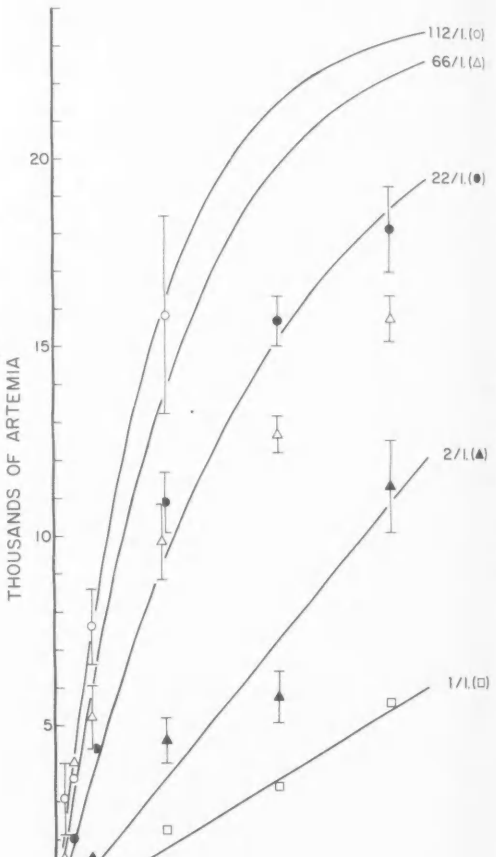

FIGURE 1.—The number of *Artemia* in digestive tracts for different density levels in the water and for different feeding durations. The lines for 1 and 2 *Artemia*/liter were calculated from equation (3) and the lines for 22, 66, and 112 *Artemia*/liter were calculated from equation (4). The symbols associated with each line show averages and standard errors for the trials in that density series. Standard errors smaller than 450 are not shown.

average capacity might well be less than 32% of weight for the asymptotic number specified. The asymptotic number, which was most strongly influenced by the trials at 22 *Artemia*/liter, may slightly underestimate the total number that can be ingested because of losses by defecation.

DISCUSSION

It is evident that *Artemia* adults approximate the smaller crustacean sizes utilized by the mackerel and that the fish resorts to filter feeding to increase the rate of consumption as density exceeds some level where particulate feeding becomes relatively inefficient. The ecological meaning of this feeding pattern is indicated by considering the resulting relation between food density and rate of food accumulation in the digestive tracts in respect to 1) the daily nutritional requirement of the species, 2) the density levels of crustaceans in the sea, and 3) the feeding rates of the northern anchovy (*Engraulis mordax*).

Hatanaka et al. (1957) showed that *S. japonicus* in coastal regions of Japan tend to utilize small fish in late summer and autumn but to rely largely on euphausiids and other crustaceans of similar size in other seasons. They concluded that mackerel a little over 1-year-old and averaging 149 g in weight required 8% of their body weight per day in crustaceans to sustain the growth rate observed in nature, which was estimated as 0.42% of body weight per day. The feeding functions derived in the present study indicate that the times required for the mackerel to obtain this daily requirement at the *Artemia* densities tested, or their equivalent for euphausiids, would be

Artemia/liter	1	2	22	66	112
Euphausiids/liter	0.7	1.3	15	44	75
Minutes	97	49	17	10	7

The equivalent densities for euphausiids are given on the assumption that the mackerel feeding rate is keyed to concentration in terms of biomass rather than to numbers per unit volume as such. Euphausiids near the surface at night in the eastern Pacific, largely *Euphausia pacifica*, average 6 mm in body length (O'Connell, 1971), and individuals of this length are 3 mg wet weight (Lasker, 1966), or 50% more than the *Artemia*.

The feeding times given above are relatively short, but the *Artemia* densities are much higher than those reported for comparable organisms in the sea. Brinton (1962) showed average densities of *E. pacifica*, largely juveniles, to be about 0.02/liter near the surface at night off southern California. O'Connell (1971) showed an average of 0.03/liter over much the same region, with perhaps 5 to 10% of the area having densities approaching 0.1/liter at any one time. These estimates would be elevated, perhaps doubled, if other large crustaceans were added on a biomass equivalent basis. The highest of these area densities would enable the mackerel to obtain its daily nutritional requirement in about half a day of particulate feeding, but the more commonly prevailing level would not permit the mackerel to obtain its requirement within the space of a day.

In all probability the mackerel obtains much of its needs from euphausiids and other crustaceans of similar size, but there is good evidence that it depends to some extent on larger organisms, such as fish up to one-third of its own body length (Hatanaka and Takahashi, 1960), to secure the daily requirement over a reasonable length of time. Though stomachs tended to be fuller and growth better during the season when the mackerel feeds primarily on fish (Hatanaka et al., 1957), it must be remembered that the 8% daily feeding requirement used here pertains to maintenance and growth when euphausiids were the primary food. If the feeding rates indicated for higher densities of *Artemia* apply for biomass equivalents of much larger organisms, the large capacity of the mackerel suggests that relatively infrequent encounters with such organisms would sustain the daily requirement in an average sense. The present study and that of Kariya and Takahashi (1969) indicate that feeding can be expected to continue towards full capacity regardless of state of fullness when food becomes available.

Though mackerel may have to depend in part on larger organisms, it is possible that the food

potential of the larger crustaceans, and even very young fish, is greater than indicated by average area densities. The definite filtering response of the mackerel, which appears to be an adaptation for capturing the smaller organisms it utilizes at a greater rate than would be possible by biting activity when density is high, implies that high densities are a factor of some consequence in the feeding ecology of the species. One possible explanation is that the various kinds of food organisms tend to be distributed contagiously, with aggregations of considerably higher density than reflected by area averages. As Ivlev (1961) demonstrated with carp fry, feeding rate can be expected to increase with degree of aggregation for a fixed quantity of food organisms. Euphausiids have been observed in schools and breeding swarms (Brinton, 1962). More than likely the filtering response is evoked in mackerel with empty or near-empty stomachs by densities not much above the equivalent of 1 or 2 *Artemia*/liter, where rate of effective biting must already be on the order of 60 or more per minute. At 4 to 5 *Artemia*/liter the daily nutritional requirement could be obtained in less than 45 min of filter feeding.

Whereas *Artemia* adults represent the smallest organisms consumed by the mackerel, they represent the largest organisms commonly consumed by the anchovy (Loukashkin, 1970); the latter also consumes phytoplankton and crustaceans less than 1 mm in length by filter feeding. The wet weight quantities of *Artemia* adults consumed at different densities (Table 5), based on the present study for the mackerel and on Leong and O'Connell (1969) and O'Connell (1972) for the anchovy, suggest the differences in utilization and nutritional value of large crustaceans for equivalent age groups of the two species.

The anchovy requires far less food than the mackerel to meet its daily nutritional requirement, and can obtain the necessary quantity in about 20 min when *Artemia* adults are at densities of 1 or more per liter. In this same period the mackerel consumes more than the anchovy at all densities, but not enough to satisfy the daily requirement. When considered in terms of the weight of the two fish, the greater quantities consumed by the mackerel have a relatively lower nutritional value than those consumed by the anchovy, except, perhaps, at very high densities.

TABLE 5.—Comparison of *Artemia* adults consumed (mg wet weight) by the 1-year-old mackerel and anchovy for different density levels of *Artemia* in the water.[1]

Item	Mackerel	Anchovy
Age in years	1+	1–
Weight ± g	147	4
Nutritional requirement:		
Percent body weight	8	6.8
mg	11,784	270
Minutes of feeding for nutritional requirement at:		
1 *Artemia*/liter	97	20
5 *Artemia*/liter	35	20
Mg *Artemia* consumed in 20 min with *Artemia* at:		
0.1 *Artemia*/liter	240	~152
1 *Artemia*/liter	600	270
5 *Artemia*/liter	9,600	270
Mg *Artemia* consumed/g fish weight in 20 min with *Artemia* at:		
0.1 *Artemia*/liter	1.6	~38
1 *Artemia*/liter	17	68
5 *Artemia*/liter	65	68

[1] Calculations for the anchovy at age 1+ and weight 7 g show the nutritional requirement and amounts consumed in 20 min at 1 and 5 *Artemia*/liter to be 475 mg, but all other values are the same as for the 4-g anchovy.

The extreme difference in quantities consumed by the two species at high densities is attributable to the filtering capability of the mackerel, and the failure of the anchovy to filter feed on the larger crustaceans, regardless of density. No meaning can be attached to the small difference at the lowest density level because calculation of the values involved considerable extrapolation. It is nevertheless probable that the anchovy tends to remove large crustaceans at a lower rate than the mackerel at such levels. O'Connell (1972) showed that the feeding activity of the anchovy is likely to be divided between these and the smaller crustaceans captured by filtering if the larger organisms are less than about 5 to 8% of the dry weight of total zooplankton concentration.

From the above considerations it is tentatively hypothesized that the individual mackerel generally utilizes a greater proportion of the large crustaceans in the sea than does the individual anchovy, but that the proportion utilized generally has a relatively low nutritional value for the mackerel.

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COLOR PATTERNS OF SPINNER PORPOISES (*STENELLA* CF. *S. LONGIROSTRIS*) OF THE EASTERN PACIFIC AND HAWAII, WITH COMMENTS ON DELPHINID PIGMENTATION

WILLIAM F. PERRIN[1]

ABSTRACT

In this paper, the second of a series on the morphology of small pelagic delphinids by the author, the color patterns of forms of a tropical spinner porpoise *Stenella* cf. *S. longirostris* (Gray) 1828 from the far eastern Pacific, from the waters between North America and Hawaii, and from Hawaiian waters are described and illustrated. The patterns can be analyzed in terms of discrete component systems, and most geographical variation appears to be in a "dorsal field system" overlying a basic general pattern. The overlay is darkest and most extensive in the easternmost form considered and lightest and least extensive in the Hawaiian form. The color patterns of three other delphinids, *Stenella graffmani*, *Delphinus* sp., and *Tursiops truncatus* are analyzed with the component approach, and possible pattern element homologies are defined.

During the course of collecting materials and data for population studies of porpoises involved in the seine fishery for tunas in the eastern tropical Pacific (Perrin, 1970a), I have during the last several years had the opportunity to observe and, less often, to photograph the color patterns of a large number of small pelagic delphinids of several species. Emerging patterns of variation and their possible implications for the systematics of these very poorly known mammals have prompted me to undertake detailed analyses of this body of observations. I have previously (Perrin, 1970b) described the color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* (Lönnberg) 1934. The primary purpose of this paper is to describe the ontogeny and geographical variation of the color patterns of spinner porpoises of the eastern tropical Pacific and Hawaii. Some description is included also of variation in the shape of the dorsal fin and correlated features.

The study is based on observations on 157 specimens from the eastern Pacific (Figure 1), of which 41 were photographed, and on photographs and observations of approximately 35 wild and captive animals from Hawaiian waters. Many of the specimens, including most of those from the far eastern Pacific east of Clipperton Island, were examined minutes after capture; others were examined after being held in frozen storage for up to 8 months. Degree of sexual development was determined by histological examination of gonads, with the exception of the large male (Figure 8) from Acapulco, of which only a photograph is available and which was undoubtedly a mature male. Skeletons of specimens of many of the animals illustrated were placed in museums, and the museum numbers are given in the figure captions.

The spinner porpoise of the far eastern Pacific has been referred to *Stenella microps* (Gray) 1846 (Miller and Kellogg, 1955; Hester,

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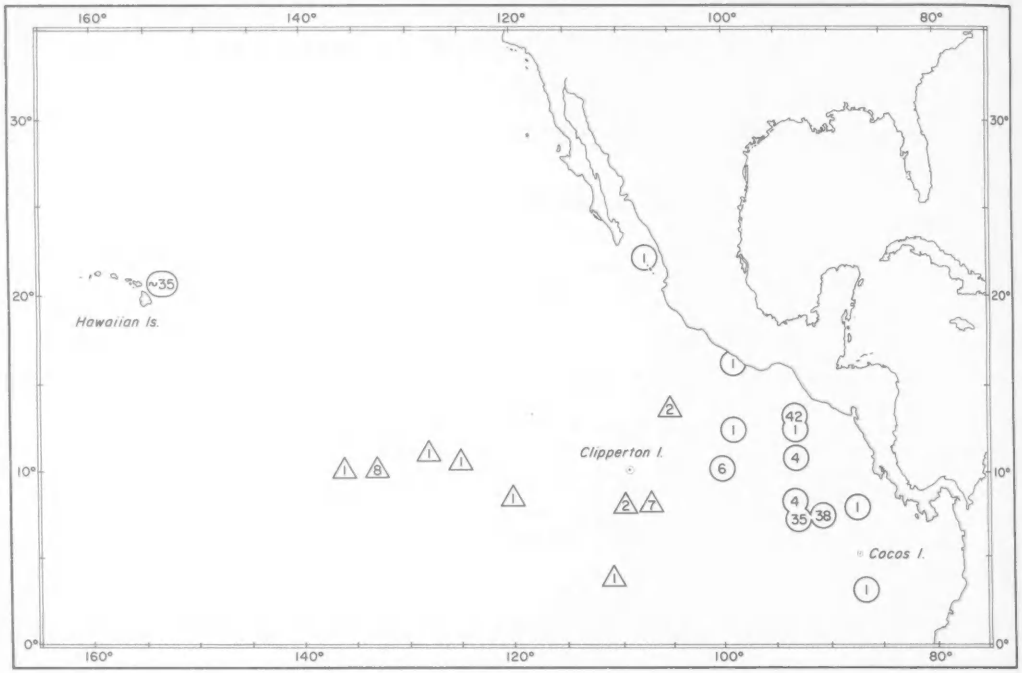


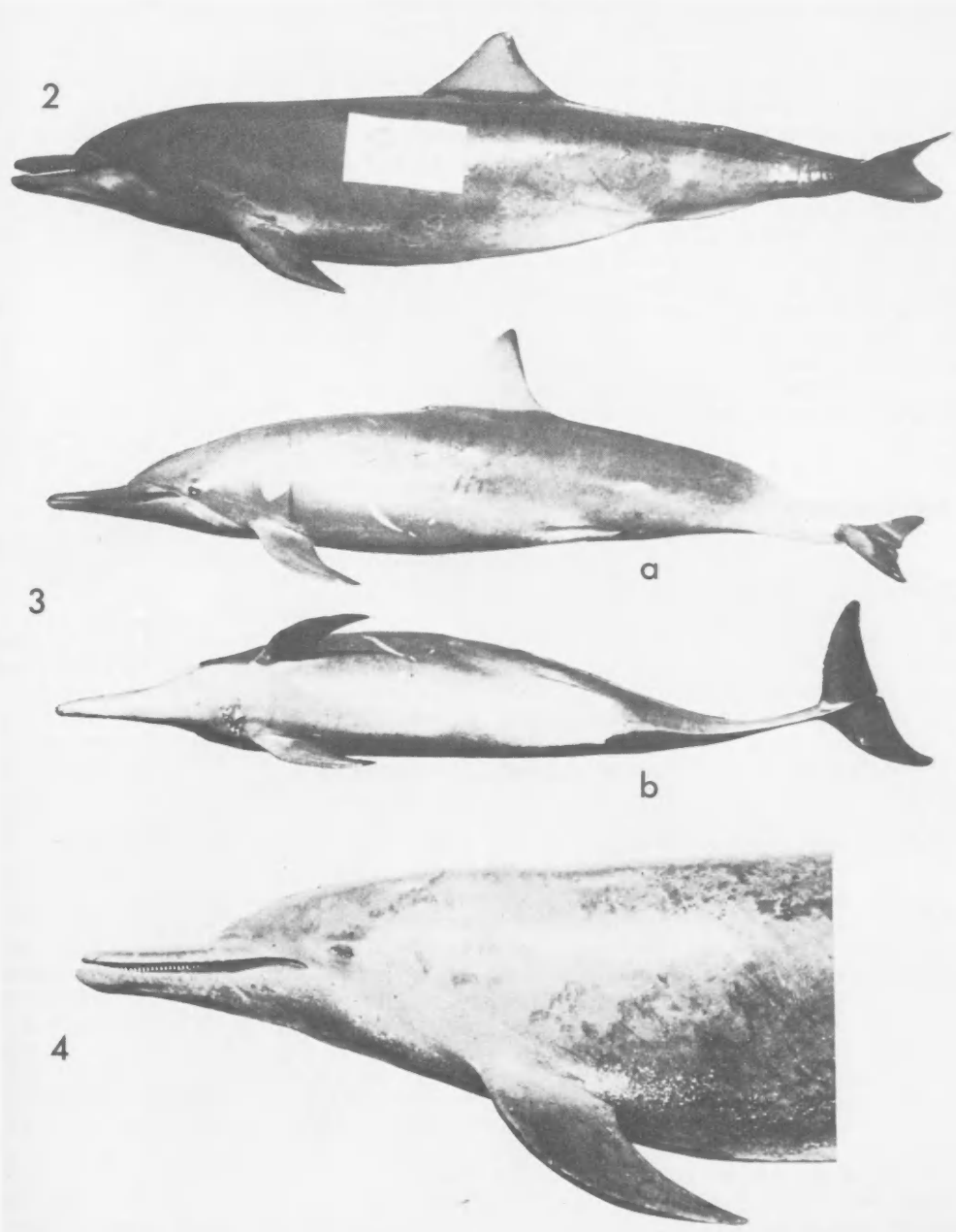
FIGURE 1.—Localities and numbers of specimens examined. Circles in eastern area indicate "eastern spinners"; triangles indicate "whitebelly spinners."

Hunter, and Whitney, 1963; Nishiwaki, 1967; Pilson and Waller, 1970), but others regard *S. microps* as a synonym of *S. longirostris* (Gray) 1828 (Hershkovitz, 1966; Rice and Scheffer, 1968; Harrison, Boice, and Brownell, 1969). The spinner porpoise of Hawaii has been referred to *S. longirostris* (Hershkovitz, 1966; Nishiwaki, 1967; Tomich, 1969) and to *S. roseiventris* (Wagner) 1853 (Brown, Caldwell, and Caldwell, 1966; Fraser, in Morris and Mowbray, 1966; Rice and Scheffer, 1968). The type localities for *S. microps* and *S. longirostris* are unknown; *S. roseiventris* was described from the Banda Sea, Indonesia. The spinner porpoise of the far offshore areas of the eastern Pacific—called "whitebelly spinner" by fishermen—has not to my knowledge been previously described or referred to any named species. No critical review of the

FIGURE 2.—Calf of eastern spinner. Male, 105 cm total length, from lat 10°30'N, long 92°56'W, April 4, 1968. Perrin field no. CV83; specimen not saved. Shape of dorsal fin is distorted by angle of photograph, should be higher. Photographed minutes after death.

FIGURE 3.—Lateral (a) and ventral (b) views of subadult eastern spinner. Female, 166 cm, from 21°43'N, 106°47'W, February 17, 1967. Marine Mammal Biological Laboratory (Seattle) field no. 1967-102. Skeletal specimen in MMBL collection. Photographed minutes after death.

FIGURE 4.—Adult eastern spinner. Female, 166 cm, from 12°51'N, 93°18'W, April 9, 1968. Perrin field no. CV7; specimen not saved. Photographed minutes after death.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genus has been accomplished since True's work on the Delphinidae published in 1889, when the existence of spinner porpoises in eastern Pacific and Hawaiian waters was not yet known. Evidence presented below concerning geographical variation in pigmentation supports the concept of a single species, highly variable geographically, but taxonomic and nomenclatorial decisions must be based on adequate review of osteological characters, as well as on a broader range of external characters than is considered here. The use of *Stenella* cf. *S. longirostris* therefore is provisional pending the outcome of more extensive studies underway by me and others. A similar situation obtains for the spotted porpoises, and use here of *Stenella graffmani* for the spotted porpoise(s) of the eastern Pacific is also provisional.

DEVELOPMENT AND INDIVIDUAL VARIATION

This account of ontogeny is divided into two parts, one describing development of color pattern as inferred from specimens from the more easterly, relatively nearshore population(s) of spinner porpoise referred to below as the "eastern spinner," and another for specimens of the "whitebelly spinner" of the more westerly, farther offshore areas of the eastern Pacific (Figure 1).

EASTERN SPINNER

Length at birth is 75 to 85 cm (Harrison et al., 1969). The smallest specimen examined was 80 cm long. The smallest specimen photographed was 105 cm long (Figure 2). At this size, the animal is predominantly dark gray. The gray of the dorsum grades imperceptibly into white around the genital region and in a smaller area in the axillary region. A dark gray flipper band from flipper base to the eye-gape region is demarcated above by a narrow, very light line running from behind the posterior insertion of the flipper to the eye and below by a sharp boundary with a light gray gular region. The boundary between the two shades of gray runs forward between the eye and the end of the gape, becoming obscure in the furrow at the base of the melon. The very light gray below grades anteriorly into darker gray, so that the upper and lower sides of the snout are of about the same shade as the dorsal field. The gape is edged with very dark gray sharply delineated above for about the last third of the gape and below for about the last half of the gape but grading distally above and below into the generally dark gray of the snout. A small eye patch of similar shade is present, and a narrow eye stripe, also of dark gray, runs from the eye patch forward to join the gape mark near the apex of the melon. A similar mark extends from the blowhole to the apex. The margin of a very faintly defined dorsal cape (not visible in the photographs) runs from near the apex of the melon to behind the dorsal fin, passing high over the eye and dipping slightly below the fin to yield a saddle effect discernible only upon very careful scrutiny of a freshly caught animal. Low on the side and adjacent to the genital slit, an elongate, smudge-like mark extends obliquely for several centimeters along a line that if extended in both directions would run from the eye to behind the anus. All appendages are on both surfaces the same gray as the dorsum. The major point of individual variation in animals of this and larger size is in the extent of the ventral and axillary white areas; in some individuals they are larger and may even be confluent, with the dorsal margin extending back from the axillary area to run into the higher genital white area.

The pattern persists as described into subadulthood (subadult being defined as an animal of adult or near-adult size but sexually immature) without change aside from overall darkening (Figure 3). In subadulthood the margins of the ventral and axillary white areas begin to become speckled, and in adults (Figures 4, 5, 6, 7, 8, and 9) the dorsal field, by now very dark gray, appears to encroach on the white areas with spots and blotches to yield a very speckled appearance below (Figure 10). As in younger animals, the major feature subject to individual variation appears to be the extent of the white areas, although in no adult specimens examined were the genital and axillary areas confluent.

FIGURE 5.—Adult eastern spinner. Female, 160 cm, from 10°30'N, 92°56'W, April 12, 1968. Perrin field no. CV81; specimen not saved. Photographed minutes after death.

FIGURE 6.—Adult eastern spinner. Female, 169 cm, from 10°30'N, 92°56'W, April 12, 1968. Perrin field no. CV82; specimen not saved. Photographed minutes after death.

In the specimens with largest white areas, the region corresponding to that of confluence in some younger specimens was dark gray thickly peppered with light gray spots (Figure 6). In some adults, the gular area is also flecked with light spots (Figure 4). In all adults the degree of contrast between the flipper band and the gular region is much reduced over that in younger animals. The cape remains obscure (see photograph of specimens in water in Perrin, 1968). The oblique mark adjacent to the genital region is obliterated in most adults, but in some can still be faintly discerned (Figure 6). The thin light gray line delineating the upper margin of the flipper band may in adults be prominent or so faint as to appear absent.

In adult males, the dorsal fin is canted forward to a greater or lesser degree (Figures 7, 8, and 9). Development of this feature is correlated with development of a protuberant keel, composed of connective tissue, just posterior to the anus. The function of these features is unknown. However, comparison of the habits of this spinner with those of the Hawaiian spinner, in which the features are very weakly developed (see below), provides a basis for a deductive hypothesis. In the eastern Pacific, spinners commonly occur together with spotted porpoise (*S. graffmani*) in mixed schools comprised of several hundred, or even thousands, of individuals of each species. In Hawaiian waters, spinners and spotted porpoise [there referred to *S. attenuata* (Gray)] do not occur in mixed schools (personal communication from K. S. Norris). In Hawaiian waters, then, most interspecific contacts could be assumed to be head-on and made at some distance, while in the mixed schools of the eastern Pacific interspecific contacts must be relatively more frequent, made at shorter distances, and for the most part lateral. It can be hypothesized that the features function in species recognition in a sexual context, perhaps, for example, to insure that oestrous females make advances to males of the proper species.

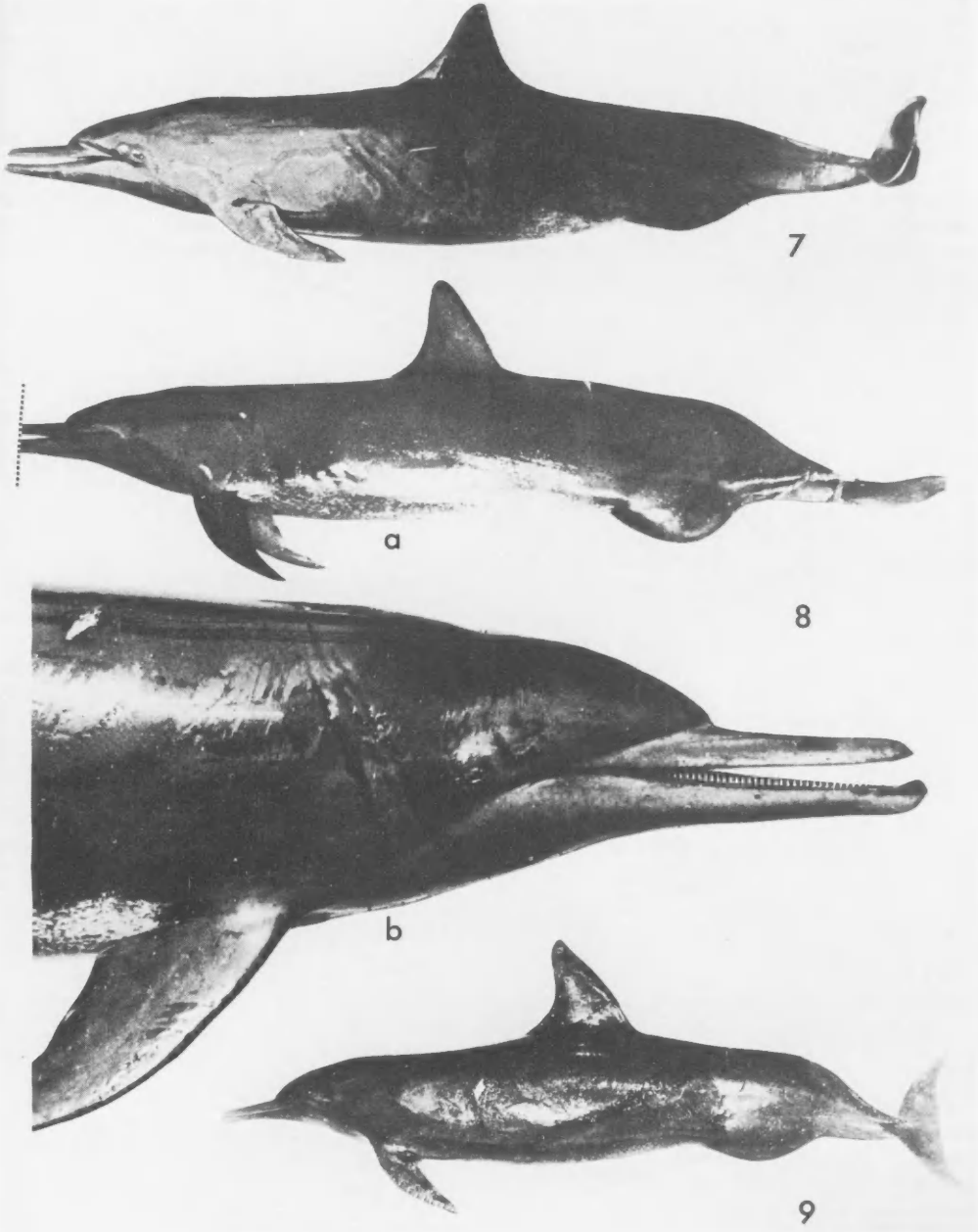
FIGURE 7.—Adult eastern spinner. Male, 175 cm, from 3°N, 87°W, July 19 or 20, 1970. Perrin field no. WFP47; U.S. National Museum no. 396026 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 8a and b.—Adult eastern spinner. Male from off Acapulco, Mexico. Photographed soon after death. Specimen not saved.

FIGURE 9.—Adult eastern spinner. Male, 186 cm, from 12°20'N, 92°53'W, March 10, 1968; San Diego Natural History Museum no. 21427 (complete skeleton and cast). Photographed in frozen state after several months in frozen storage.

WHITEBELLY SPINNER

In this animal the ventrum is white. In all young specimens examined, the axillary and genital white regions were confluent (Figure 11) as in only some young eastern spinners. Again, not much change occurs in the pattern until late subadulthood (Figures 12, 13, and 15) when the margin of the ventrum becomes speckled. The main point of difference between these animals and the eastern specimens, aside from the larger ventral light areas, is that there is much greater contrast between the dorsal cape and the lateral field. The cape can even be discerned in some of the photographs of frozen specimens (Figure 13). In some subadults (Figure 13) an anteriorly narrowing dark gray mark can be seen in the area between the flipper insertions. Other differences between this and the eastern form are discussed below. As in the eastern spinner, individual variation among adults (Figures 16, 17, 18, 19, 22, and 23) is most pronounced in extent of the light ventrum, but the lower end of the range is about equal to the upper end for the eastern spinner. Also again, there is considerable variation in intensity of speckling (compare Figures 16 and 22), and the supra-flipper-band stripe may be effectively absent (Figure 19). The flippers are usually dark on both sides, but may be speckled above (Figure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22) and/or below (Figure 21). The oblique mark adjacent to the genital region is obliterated in some adults, but in others (Figure 23) is very clearly delineated.

FIGURE 10.—Close view of genital region of adult male eastern spinner depicted in Figure 9.

FIGURE 11.—Lateral (a) and ventral (b) views of calf of whitebelly spinner. Female, 105 cm, from 8°N, 109°45'W, March 5, 1969. Perrin field no. PQ11; U.S. National Museum 395601 (complete skeleton). Photographed frozen after approximately 1 month in frozen storage.

FIGURE 12.—Subadult whitebelly spinner. Female, 129 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP58; U.S. National Museum 396036 (complete skeleton). Photographed after frozen for several months and thawed in water.

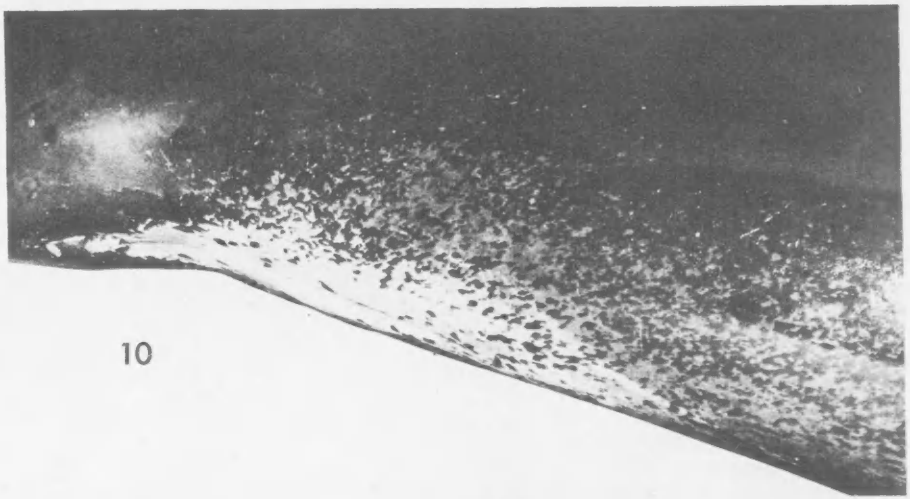
GEOGRAPHICAL VARIATION

Very young specimens of the Hawaiian spinner (Figure 24, and Figure 7 in Perrin and Hunter, 1972) were not available for examination nor was it possible to determine with certitude the degree of maturity of most of the animals seen. One large male observed (PUKA at Sea-life Park in Waimanalo, Oahu), however, has been in captivity for 5 years and can be presumed to be adult. The major differences between the Hawaiian spinner and the whitebelly spinner of the eastern Pacific are that in the Hawaiian animal the light ventrum extends dorsad nearly to the level of the eye, as it does in its extreme expression in the whitebelly spinner, and is not speckled at the margin. The dorsal fin becomes increasingly erect with development, but is always at least slightly falcate, and the ventral keel associated with triangular and canted fins in the eastern Pacific spinners is all but absent. All contrasts are on the average more pronounced: between cape and lateral field, flipper band and gular area, gape mark and underside of lower jaw. The ventral margin of the cape follows a convex smooth curve over the eye in the whitebelly spinner but dips over the eye in the Hawaiian form.

The differences among the whitebelly, eastern, and Hawaiian spinners are summarized in Table 1. These differences appear to be based primarily in differential development. The small subadult of the whitebelly spinner (Figures 12 and

TABLE 1.—Summary of some external features differing between adults of Hawaiian, whitebelly, and eastern spinner porpoise.

Feature	Hawaiian spinner	Whitebelly spinner	Eastern spinner
Contrast of cape with lateral field	Very pronounced	Clearly discernible	Effectively absent
Ventral margin of cape over eye	Dips	Smooth curve, no dip	Obscure
Ventral white field	Extends dorsad nearly to level of eye; margin smooth	Extends dorsad variably nearly to level of eye; margin speckled; genital and axillary areas confluent	Restricted to discrete genital and axillary areas of varying extent; margins speckled
Black snout tip	Present	Variable	Absent
Contrast between flipper band and gular region	High	High to medium	Low
Spots in gular region	Absent	Variable	Variable
Flippers	Dark	Dark or speckled	Dark
Dorsal fin in adult male	Falcate	Falcate to triangular	Triangular to canted
Protuberant ventral keel in adult male	Absent	Small to medium	Small to large



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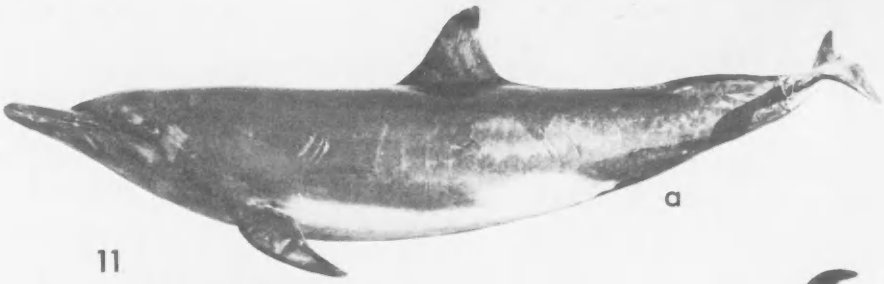

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13) more closely resembles the Hawaiian spinner than does the adult, in that the margin of the ventral white field is relatively smooth. The pattern of the fetus of the eastern spinner (Figure 25) is also very close to the Hawaiian pattern, with the tripartite effect of cape, lateral field, and high ventral field being very pronounced. The question of which sort of developmental cline is involved, paedogenesis to the west or gerontogenesis to the east, is however yet an open one and must be settled by consideration of additional lines of morphological and zoogeographic evidence.

Pattern component analysis.—Comparison of the color pattern of a partially albinistic subadult whitebelly spinner (Figure 14) with that of a normally pigmented individual of the same sex and nearly the same length (Figure 13) affords insight into the mechanisms of pattern formation. In the lighter-than-normal animal, the cape, eye patch and stripe, gape mark, dorsal fin, and flukes are as in the normal specimen. The lateral field, flipper band, and oblique genital mark are obscure, and the flippers are white on both surfaces. White brushings sweep up from the edge of the cape at about midlength toward the dorsal fin. From these facts, the inference can be made that the full normal pattern is the result of the combined effect of two independent pigmentation systems, one involving the cape and accessory stripes, eye and gape marks, dorsal fin, and flukes, and the other involving lateral field, flipper band, and flippers. While the genital mark is not apparent in the albinistic animal, the developmental pattern of obliteration through development of the lateral field suggests that it belongs to the cape system. The difference among the Hawaiian, whitebelly, and eastern spinners can be interpreted schematically in terms of these hypothetical systems (Figure 26), allowing a clearer picture to emerge of the possible patterns of geographical variation involved. Since the lateral field appears in this sense to be the lateral portion of a more extensive dorsal field overlaying the cape, it is referred to below as an aspect of a "dorsal field overlay."

Among these three forms, the "dorsal field overlay" is darkest and most extensive in the easternmost form, and least so in the Hawaiian form. It is not yet known whether the three forms represent modes in a geographically continuously varying single species or two or more reproductively isolated allopatric or sympatric populations.

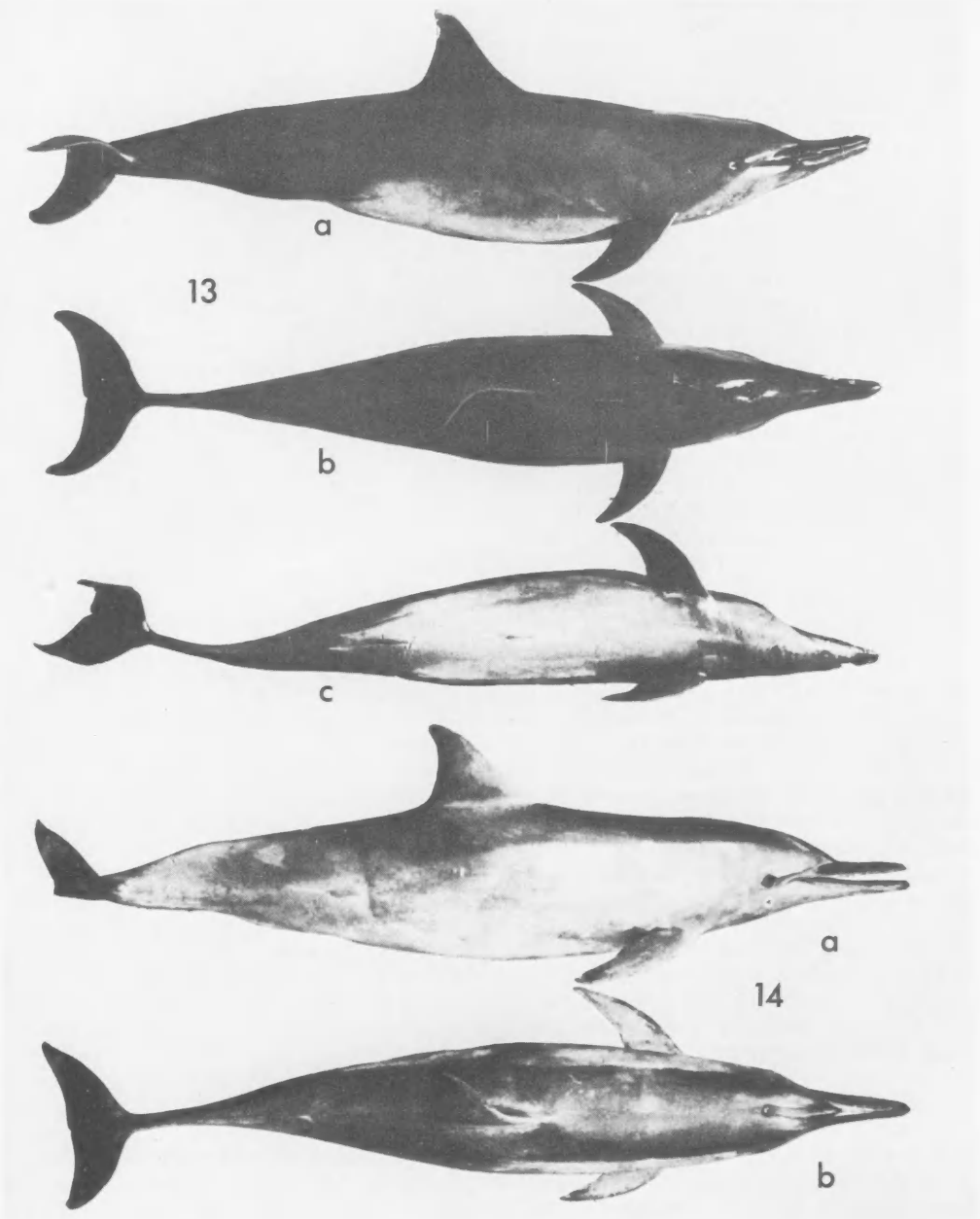
FIGURE 13.—Lateral (a), dorsal (b), and ventral (c) views of subadult whitebelly spinner. Male, 164 cm, from 9°47′N, 133°25′W, August 11, 1970. Perrin field no. WFP65; U.S. National Museum 396017 (complete skeleton). Rostrum damaged. Photographed after frozen for several months and thawed in water.

FIGURE 14.—Lateral (a) and dorsal (b) views of albinistic subadult whitebelly spinner. Male, 154 cm, from 10°19′N, 135°38′W, August 5, 1970. Perrin field no. WFP67; U.S. National Museum 396020 (complete skeleton). Compare with normally pigmented animal in Figure 13. Note dark flukes and light flippers. Photographed after frozen for several months and thawed in water.

OTHER DELPHINIDS

The color patterns of other closely related delphinids can be similarly dissected into hypothetical component systems. The patterns of three forms of which I have directly examined live or freshly captured dead specimens are analyzed in Figure 27, with an attempt to define possible homologies for the component systems among the species. As the first step in breaking down the patterns into supposedly homologous components, I attempted to define for each a cape with associated markings, similar to that in the albinistic spinner described above.

In the eastern Pacific spotted porpoise, *Stenella graffmani*, (Figure 27, top) the general cape system is very close to that of the spinners, with the cape extending farther ventrad. The dorsal overlay is less extensive than in any of the spinners, and the flipper band runs forward to the gape rather than to the eye. The area of contact between the flipper band and the gape mark in this and in similar spotted porpoise from other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parts of the world is emphasized in many individuals by a zone of lighter pigmentation (see Figures 4 and 6 in Perrin, 1970b; Figure 1 in Best, 1969; and Figure 3 in Nishiwaki, Nakajima, and Kamiya, 1965), which supports the idea of separate origin of the two marks. In the spotted porpoises, the combined pattern systems are overlaid with discrete dorsal and ventral spot systems that to greater or lesser extent obliterate them (Perrin, 1970b).

In *Delphinus* spp. (Figure 27, middle) the dorsal field overlay is less extensive anteriorly than the cape, resulting in invasion of the cape by the ventral field and yielding a four-part crisscross pattern with zones of black, buff, gray, and white. The deduction to be made is that the whitebelly region represents total lack of pigment, the buff "thoracic patch" (terminology of Mitchell, 1970) represents the color yielded by the pigment of the cape alone, the gray "flank patch" (of Mitchell) that of the pigment of the dorsal field overlay alone, and the black dorsalmost area that of the combined effect of the pigments of the cape and the dorsal field overlay. Chromatographic analysis of pigments present in the various regions and comparison of the results with those of similar tests for other delphinids would contribute to verification or rejection of the suggested homologies.

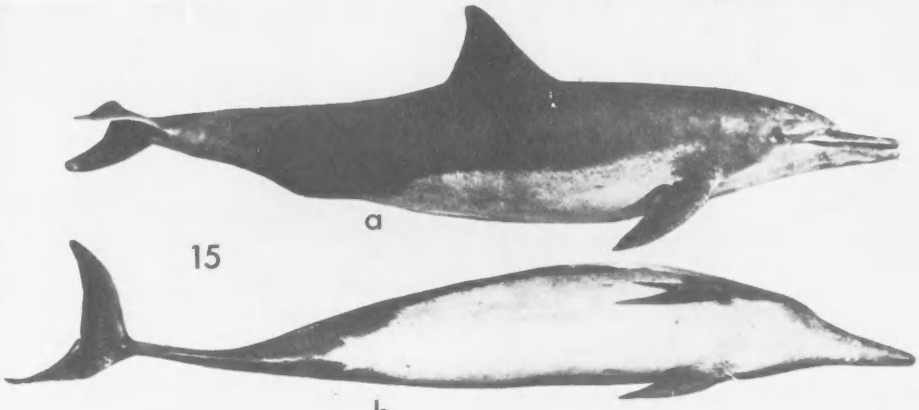
The pattern of *Tursiops truncatus* (Figure 27, bottom) is very close to that of the spinners in every respect, with the flipper band running to the eye and demarcated dorsally by a narrow light line. The dorsal field overlay of varying darkness extends ventrad to about the same degree as in the eastern spinner. Observation of wild bottlenose porpoise in the eastern temperate and tropical Pacific and examination of some of the thousands of published photographs of animals from around the world lead me to believe that the main component of geographical variation, as for the spinner porpoises, is the extent and darkness of the dorsal overlay. In Hawaiian *Tursiops* that I have observed, the ventral margin was high and sharply defined exactly as in the Hawaiian spinner.

The general cape system common to the four forms discussed above corresponds roughly to the "saddled pattern" described by Mitchell (1970) as a generalized and probably primitive pattern within the Delphinidae. The "saddled pattern" depicted in his Figure 7, however, is definitely not that of the spinner porpoises, which he included in a group of "saddled" species in his Figure 17. I concur with Mitchell in his selection of the "saddled" condition as a good candidate for a primitive pattern, insofar as his definition of that pattern category pertains to the "general cape system" described here. Lines of evidence presented here leading to this conclusion are the possession in common of a relatively invariant cape system by several delphinid species and the tendency of the cape to be partially marked, distorted, or obliterated in a varying fashion within a species or species group not so much by alteration of its intrinsic form but more by interaction with more plastic overlying systems or (as Mitchell pointed out in the case of the "spinal blaze") by subtraction through invasion by areas of nonpigmentation.

FIGURE 15.—Lateral (a) and ventral (b) views of subadult whitebelly spinner. Male, 166 cm, from 10°N, 129° or 136°W, August 10-12, 1970. Perrin field no. WFP71; U.S. National Museum 396023 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 16.—Lateral (a) and ventral (b) views of adult whitebelly spinner. Male, 169 cm, from 9°47′N, 133°25′W, August 11, 1970. Perrin field no. WFP53; U.S. National Museum 396031 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 17.—Adult whitebelly spinner. Male, 174 cm, from 9°47′N, 133°25′W, August 11, 1970. Perrin field no. WFP76; U.S. National Museum 396170 (complete skeleton). Photographed after frozen for several months and thawed in water.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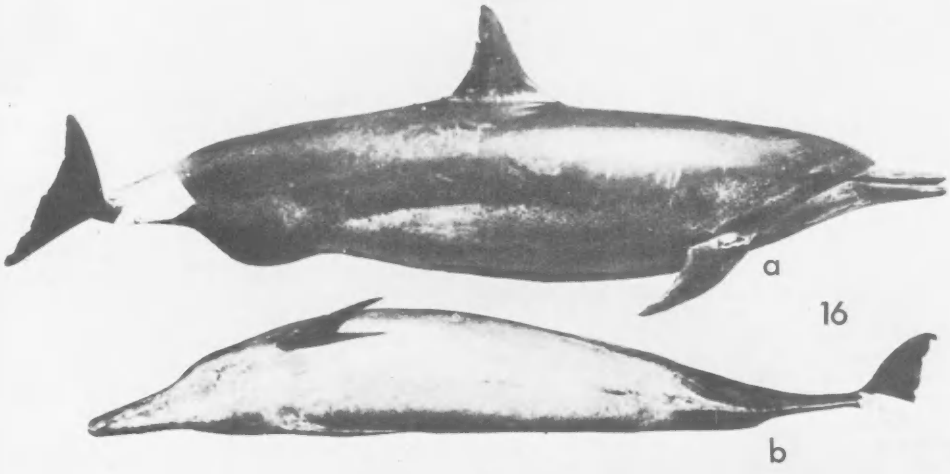
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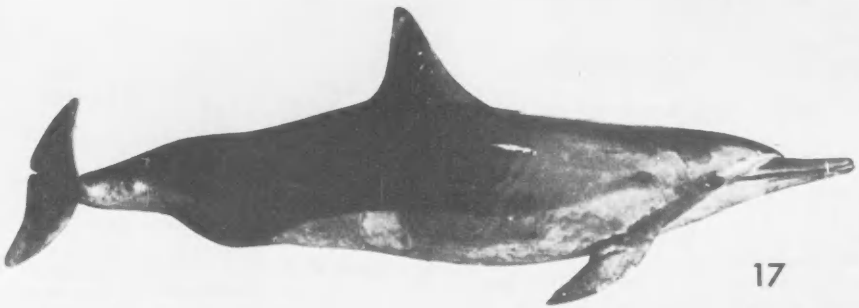
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Specimens were collected and examined through the cooperation of the owners, captains, and crews of the tunaboats *Carol Virginia, Conte Bianco, Connie Jean, Conquest, Anne M, Pacific Queen,* and *Queen Mary.* C. J. Orange, J. S. Leatherwood, and G. D. Sharp collected specimens. D. W. Rice provided the photographs used in Figure 3. J. H. Prescott provided photographs used in Figure 8. K. S. Norris provided photographs used in Figure 24, and arranged for a visit to Hawaii to observe wild and captive spinner porpoise. I am indepted to Bonnie Dalzell for the ideas concerning the possible significance of the canted fin and ventral keel in the eastern spinner. K. S. Norris, E. D. Mitchell, D. W. Rice, C. O. Handley, Jr., and D. K. Caldwell read the manuscript. E. D. Mitchell offered especially valuable criticism.

FIGURE 18.—Adult whitebelly spinner. Male, 177 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP54; U.S. National Museum 396032 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 19.—Adult whitebelly spinner. Male, 178 cm, from 10°N, 128° or 136°W, August 10-12, 1970. Perrin field no. WFP52; U.S. National Museum 396030 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 20.—Dorsal surface of flipper of specimen depicted in Figure 17.

FIGURE 21.—Ventral surface of flipper of specimen depicted in Figure 19.

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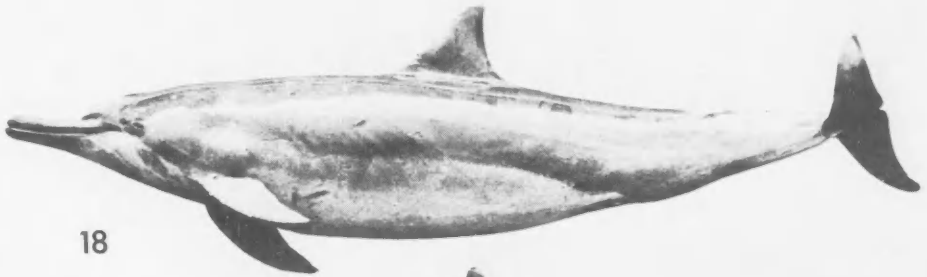

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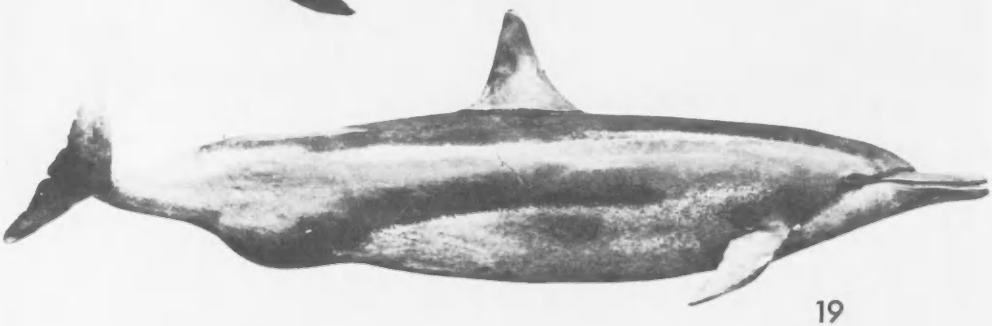

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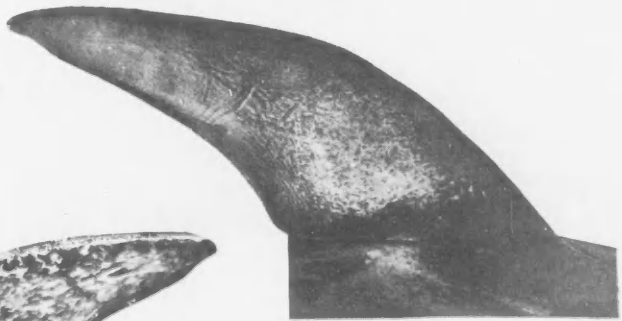

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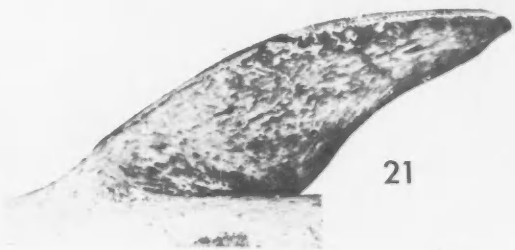

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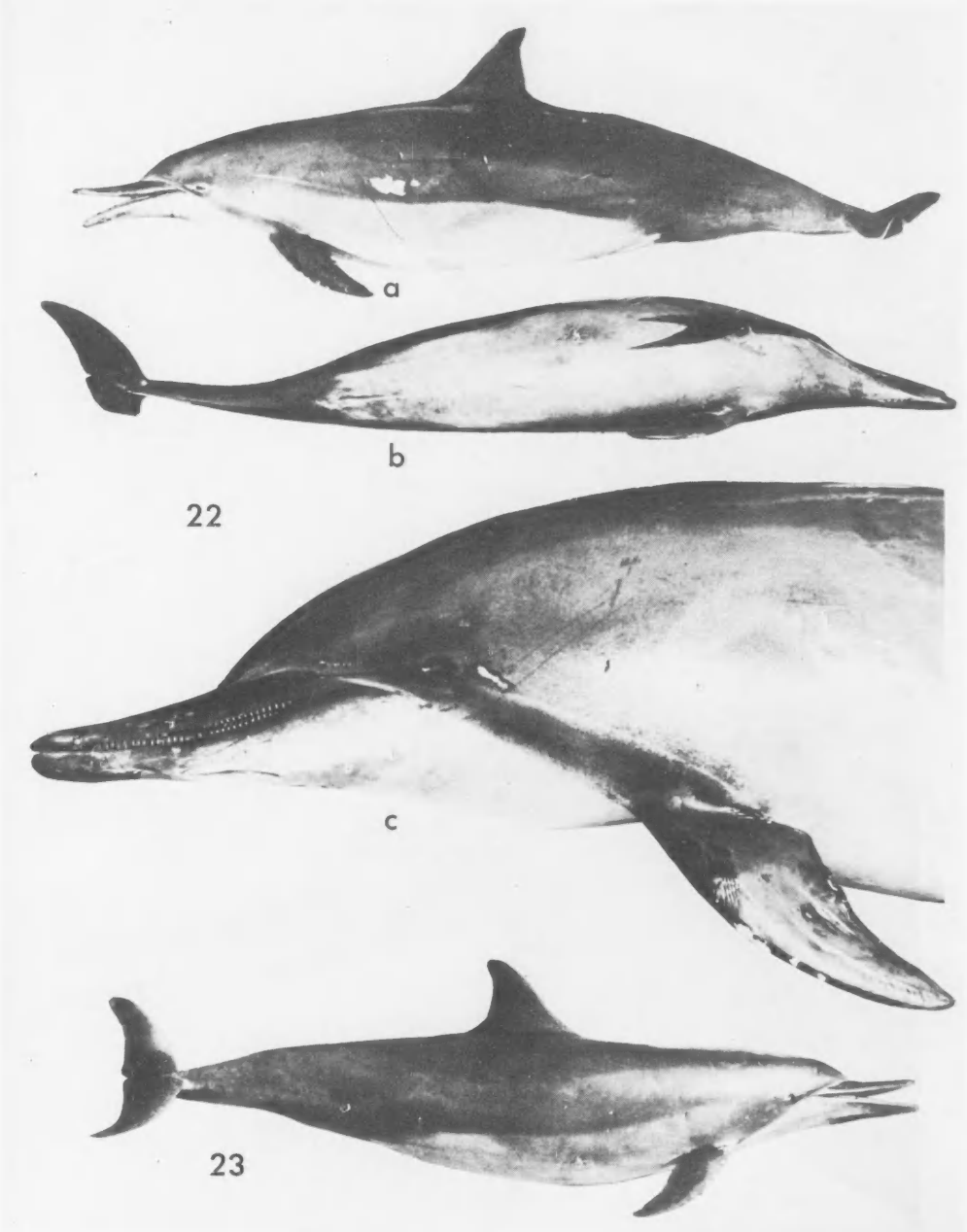
FIGURE 22.—Lateral (a) and ventral (b) views of adult whitebelly spinner. Female, 179 cm, from 3°20'N, 110° 44'W, June 24, 1970. Perrin field no. WFP79; U.S. National Museum 396173 (complete skeleton). Rostrum damaged. Photographed after frozen for several months and thawed in water.

FIGURE 23.—Adult whitebelly spinner. Female, 169 cm, from 8°19'N, 119° 15'W or 3°20'N, 110°44'W, June 11 or 24, 1970. Perrin field no. WFP80; U.S. National Museum 396174 (complete skeleton). Photographed after frozen for several months and thawed in water.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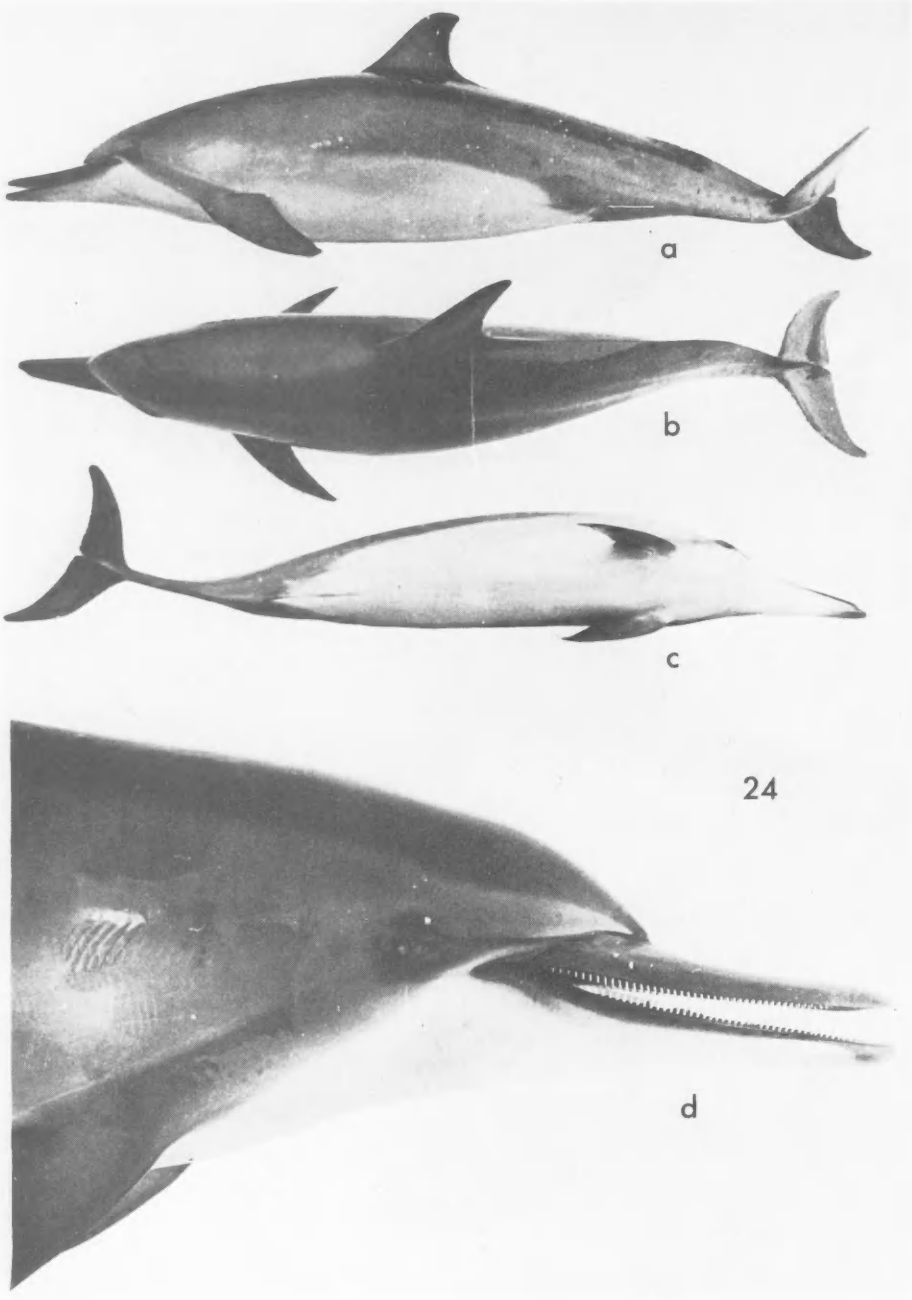
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FIGURE 24.—Lateral (a), dorsal (b), ventral (c), and close-up lateral (d) views of Hawaiian spinner porpoise. Subadult male, 179 cm, from Waikiki Beach, Oahu, May 25, 1970. Oceanic Institute field no. OI70-35; specimen stolen during preparation. Photographed 3 hours after death.

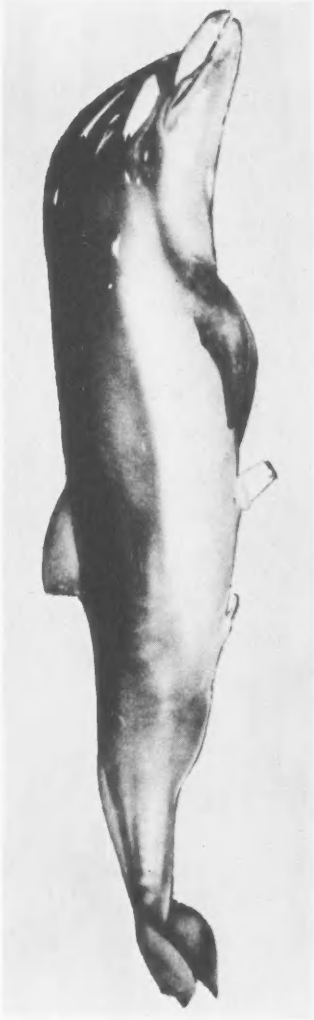

FIGURE 25.—Fetus of eastern spinner. Male, 361 mm, 640 gm, from 9°19'N, 105°20'W, November 10, 1971. Perrin field no. (of mother) WFP187. Specimen at the National Marine Fisheries Service Laboratory, La Jolla, Calif. Photographed underwater after removal from frozen adult, which had been frozen for several months and thawed in water. Dorsal fin folded, and epidermis damaged about head (white areas).

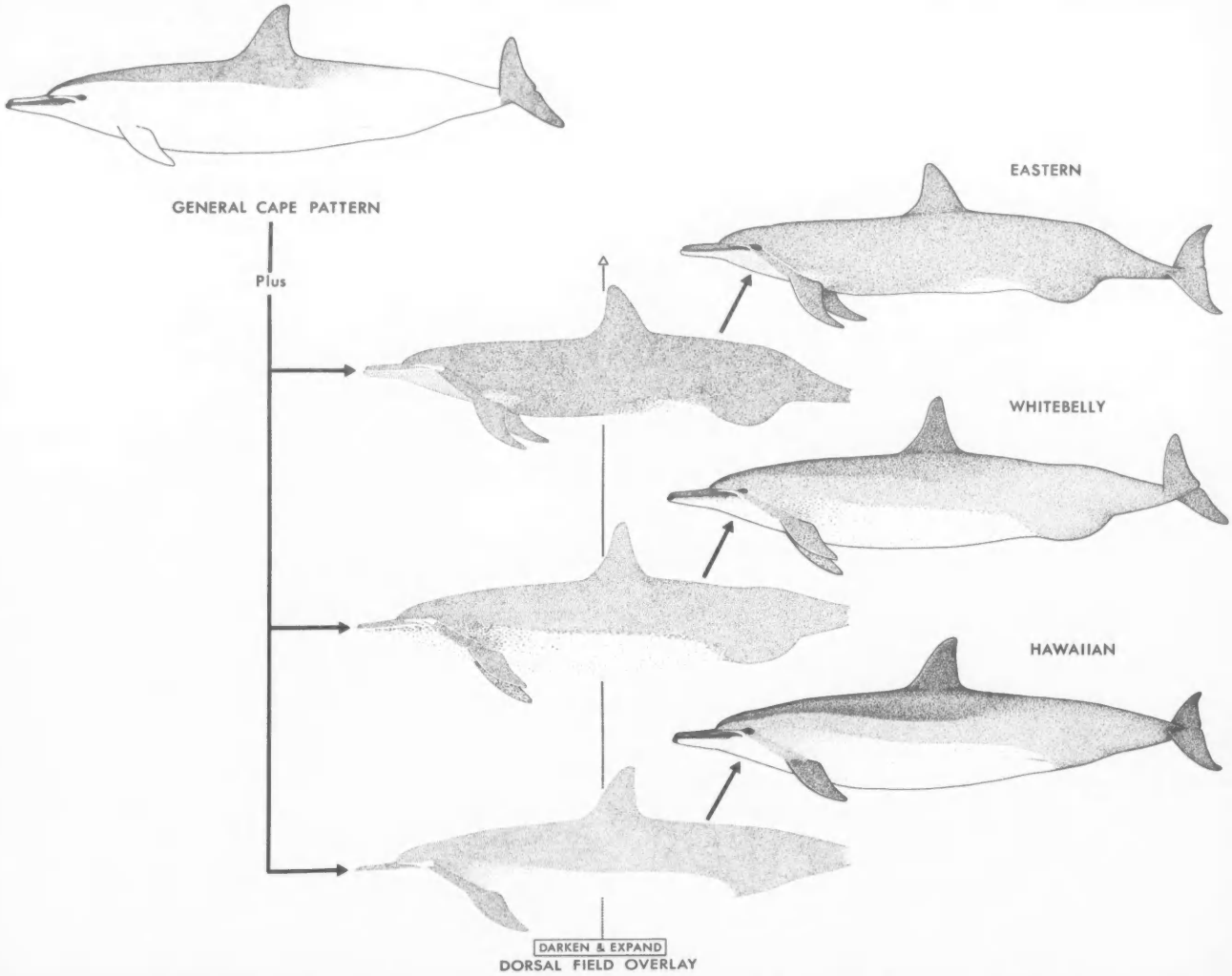

FIGURE 26.—Scheme for analysis of color patterns of spinner porpoises in terms of discrete component systems.

FIGURE 26.—Scheme for analysis of color patterns of spinner porpoises in terms of discrete component systems.

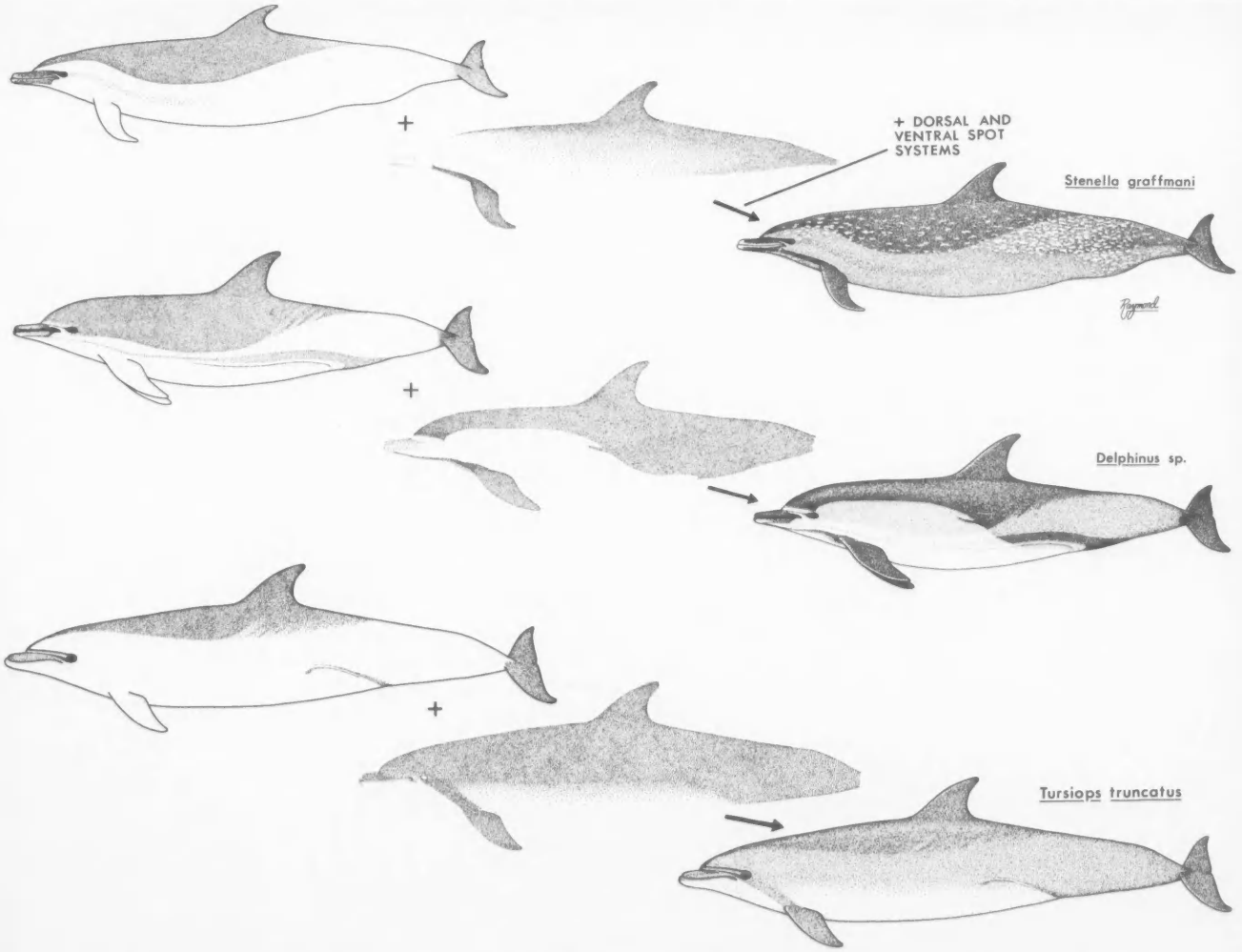

FIGURE 27.—Component analyses of color patterns of *Stenella graffmani, Delphinus* sp. (based on observations of specimens taken off southern California), and *Tursiops truncatus* (based on observations of captive specimens from southeast Atlantic coast of United States).

APPARENT ABUNDANCE OF SOME PELAGIC MARINE FISHES OFF THE SOUTHERN AND CENTRAL CALIFORNIA COAST AS SURVEYED BY AN AIRBORNE MONITORING PROGRAM

JAMES L. SQUIRE, JR.[1]

ABSTRACT

From September 1962 through December 1969, commercial aerial fish spotter pilots estimated tonnage of species observed during flights off the southern and central California coast. Observations of fish and the aircraft's flight route were recorded on special charts. These data were analyzed using 10-minute-longitude by 10-minute-latitude "block areas." A total of over 17,593 flight hours was involved, surveying 57,628 block areas—37,186 during the day and 20,442 during the night. Data from each block area were used to compute diurnal and nocturnal variation in apparent abundance and an annual index of apparent abundance.

Pacific bonito, *Sarda chiliensis*, and yellowtail, *Seriola dorsalis*, were observed in greater frequency and quantity during the day, and the northern anchovy, *Engraulis mordax;* jack mackerel, *Trachurus symmetricus*; and Pacific mackerel, *Scomber japonicus*, were observed in greater frequency and quantity during the night. Pacific barracuda, *Sphyraena argentea*, was observed in greater quantity at night but more frequently during the day.

Between 1963 and 1969 indexes of apparent abundance declined for jack mackerel, Pacific mackerel, Pacific sardine, Pacific bonito, Pacific barracuda, and yellowtail and increased slightly for the northern anchovy. The index closely follows estimates of total abundance for the Pacific mackerel, a species for which reliable estimates of total abundance are available. From observations of the catch trends in the bonito fishery, the index appears to be little affected by changes in economic demand. Its trends in apparent abundance are evident before they are reflected in catches and are useful in the evaluation of catch variations in underutilized resources.

In a search for more efficient fishing methods, many of the fisheries throughout the world that catch pelagic surface schooling species are using aircraft to locate and guide the fleet to the schools and in some cases to direct the catching operation (Cushing, Devold, Marr, and Kristjonsson, 1952). In some areas of the United States the services of the fish spotter are vital to the success of the commercial fleet which depends in part on the aircraft scouting the fishing grounds to obtain current information on the location of near-surface schooling fish (Squire, 1961). At times commercial aerial fish spotters assist the sport fishing fleet by advising them of the location of desirable marine game species.

Data obtainable by techniques of aerial observation have been used by fishery biologists to gain information on distribution and abundance of pelagic near-surface schooling fish.

Sette (1949) investigated the possibilities of aerial scouting for sardines off southern California in search of a method that would provide information useful in estimating abundance yet be free of the availability influence. Aerial scouting was conducted during the day, and commercial fishing was conducted at night. As a result the spotting data were deemed less reliable than those obtained from the commercial fishery.

Jones and Sund (1967), using commercial fish

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spotter aircraft in a search for tuna schools in the same area surveyed by a research vessel, found that the aircraft was about two and one half times more efficient than the vessel at locating fish schools. An evaluation of aircraft by the U.S. Navy, for making biological observations, indicated that for whales the frequency of sighting averaged about 20 times greater than that from ships (Levenson, 1968).

From 1956 to 1964 the California Department of Fish and Game conducted monthly survey flights along the California coast from San Francisco to Mexico. Data were published as flight reports in chart form showing the aircraft's flight track, areas surveyed, notes on species observed, and number of schools and their geographical location. Large variations in the number of schools visible over a short-time period appeared to limit the usefulness of the data, and the surveys were discontinued in 1964. The average number of schools sighted per flight was determined by Wood (1964),[2] and from these data a comparison was made of the relative abundance of northern anchovy, *Engraulis mordax*, schools for the period 1956 through 1963. Limitations on flights to nearshore areas during daylight and low search time in any one area restricted the potential of these surveys for determining the apparent abundance of the many pelagic species found off the California coast.

Fish spotter aircraft range over a large geographical area, and during these flights they may observe concentrations of several species of pelagic fish. Many times these fish are not caught for one or more reasons, such as fishing boats not equipped with proper nets, concentrations are small, species is not economically desirable, and fishing boats are not capable of reaching fish within a reasonable length of time. However, the fish spotters are able to identify these concentrations of fish.

Species commonly observed by the aerial fish spotters within the survey area were northern anchovy, jack mackerel, *Trachurus symmetricus;* Pacific bonito, *Sarda chiliensis;* Pacific mackerel, *Scomber japonicus;* Pacific sardine, *Sardinops sagax*; bluefin tuna, *Thunnus thynnus*; Pacific barracuda, *Sphyraena argentea*; white seabass, *Cynoscion nobilis*; and yellowtail, *Seriola dorsalis*.

The majority of fish spotting effort is directed toward the location and catching of jack mackerel, Pacific mackerel, Pacific bonito, Pacific sardine, and in recent years the northern anchovy. Of these five species the Pacific sardine and Pacific mackerel are most economically desirable with jack mackerel, Pacific bonito, and northern anchovy of descending importance.

To increase knowledge on the apparent abundance of pelagic near-surface marine life, the Tiburon Marine Laboratory initiated a pelagic fish monitoring program in cooperation with aerial fish spotter pilots who are active in spotting for the southern and central California coastal commercial fishery. These cooperators were individuals with specialized training and experience. When assisting the commercial fleet, fishing success is dependent upon accurate identification of schooling species by the spotters. They have considerable experience in estimating the weight of fish schools, and they are considered to be quite accurate in the estimation of weight.

There are a number of variables that affect the statistical accuracy of fish spotter data which are difficult to evaluate, such as individual difference in ability of pilots to locate fish, determine species, and estimate school size, and estimate total tonnage available in a fishing area. Variation in estimating school size probably has more effect on the data than the other variables. However, since at least five experienced observers were used in the program during each year, it was assumed that reasonable annual averages were obtained.

This report consists of an analysis of aerial fish spotter data for the period September 1962 through December 1969 to determine if, for the species commonly observed, it can be used to: (1) compute an accurate index of apparent abundance and (2) obtain a trend in the apparent abundance of pelagic near-surface species and in particular those of underutilized resources.

[2] Wood, R. 1964. Aerial surveys along the California coastline 1956 to 1963. Document V prepared for the Marine Research Committee meeting, March 6, 1964, San Pedro, Calif., 2 p. [Processed.]

METHODS AND PROCEDURES

Five fish spotter pilots were contracted to record observations of pelagic species, giving location, number of schools, estimated tonnage of each school or groups of schools, counts of large marine animals, and flight track for each survey flight. Two pilots usually covered the Santa Barbara Channel and Santa Barbara Islands north to Estero Bay and occasionally into Monterey Bay. The remaining three spotter pilots normally surveyed the area from west of Los Angeles to southwest of San Diego and occasionally offshore to San Clemente Island, Cortez Bank, and San Nicholas Island. Flight operations were conducted during daylight hours or on nights during the dark phase of the moon at elevations of 500 to 1,200 ft (152 to 365 m) above the sea surface.

TECHNIQUES OF OPERATION

Specific observation of a fish school has three phases: (1) distinguishing a school, (2) identifying the species, and (3) estimating weight of the school. The detection of near-surface schools during the day is dependent upon the pilot's ability to distinguish subtle color and light intensity differences in the water. Detection of schools at night is possible only during the dark period of the moon and depends on the pilot's ability to discern gradation of light intensity. Bioluminescence of planktonic organisms agitated by schooling fish indicates by a dull glow the location and size of the school. Species are identified during the day on the basis of a combination of two or more of the following characteristics: color of school or individual fish, shape of school, and behavior and size of individuals within the school. At night, species identification is based on shape of the luminous area and behavior of the schooling fish under undisturbed conditions, or by the behavior of the school after being subjected to a stimulus from an external source such as a flash from the aircraft's landing light.

At first observations were recorded by the pilots on small portable tape recorders. This method was unsatisfactory, and recorders were replaced with three charts covering the coastal waters from the Coronado Islands, Mexico, north to Half Moon Bay, Calif. The charts were completed by the pilots after each flight and were submitted quarterly to the National Marine Fisheries Service. Figure 1 illustrates the type of information recorded by the fish spotter pilot.

PROCESSING OF OBSERVATION DATA

Each chart was overlayed with a 10-minute-longitude by 10-minute-latitude grid, numbered according to the California Department of Fish and Game "Block area" statistical system (Clark, 1935). With the gridded chart, the observation and flight track data could be conveniently tabulated and coded for subsequent computer analysis. California Department of Fish and Game statistical code numbers were assigned to each of the 27 species of marine animals observed. The computer output grouped data by species, year, week, block area, day or night observation, number of schools, tons per school, and tons per block area. The data for block areas were later combined into 11 larger grouped block areas or "zones" lettered A through K (Figures 2 and 3). These zones were selected to outline important geographical areas where fish were commonly observed.

The following criteria were used in tabulating the data from the flight charts:

1. Groups of schools which were indicated on the flight chart as covering more than one block area were listed for each block holding part of the group. For example, if one group of schools (10 schools, 15 tons per school, total 150 tons) overlapped two block areas equally, each area was credited with having 5 schools at 15 tons per school, equalling 75 tons per block area.

2. If only one school was shown overlapping two block areas, the school was assigned to the block area having the greatest portion of the school.

3. If a large area of fish was indicated involving more than two block areas and only a total tonnage estimate made, the tonnage was credited to the block areas in proportion to area outlined.

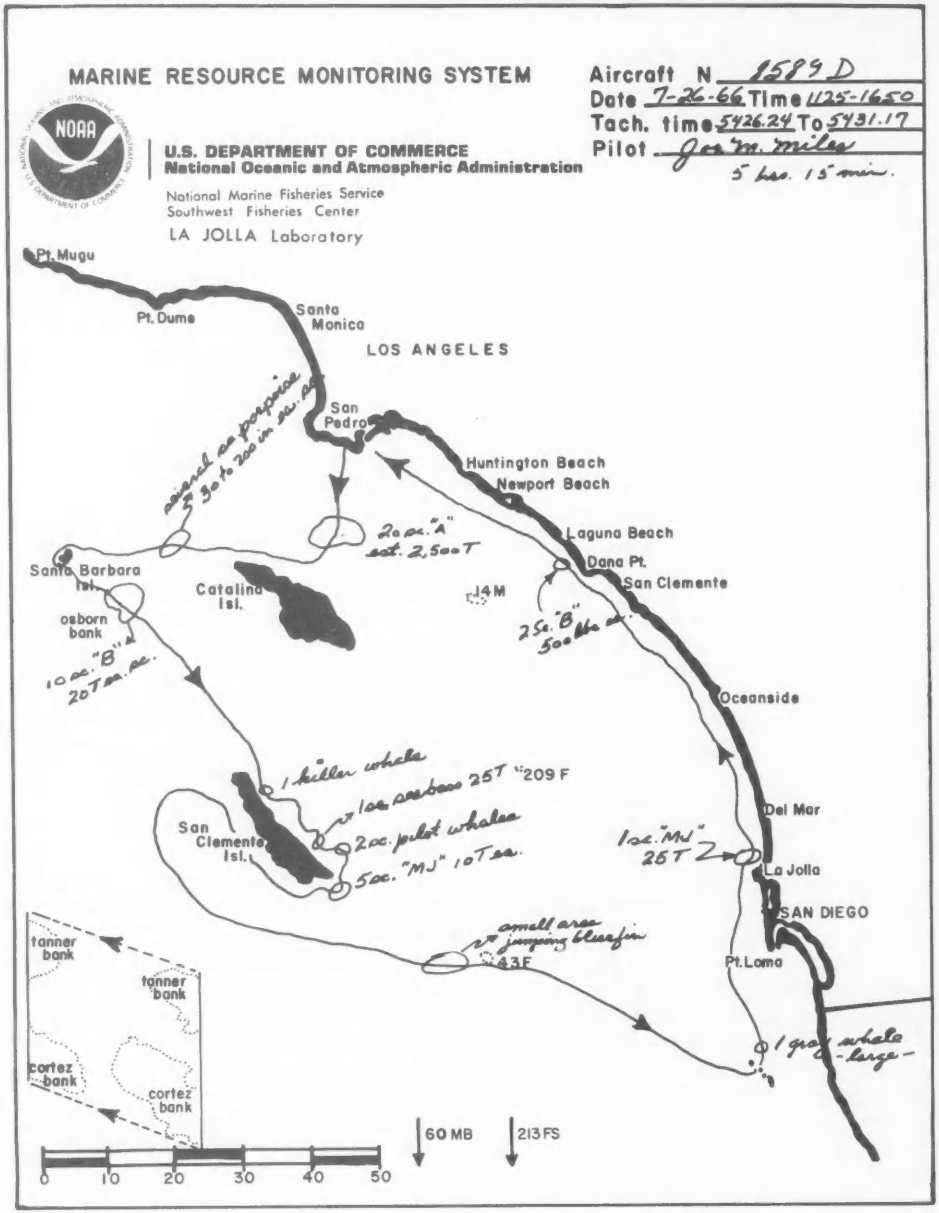

FIGURE 1.—Flight chart for southern California area showing typical flight track and fish and mammal observations. Block area grid is overlayed on chart for coding observations.

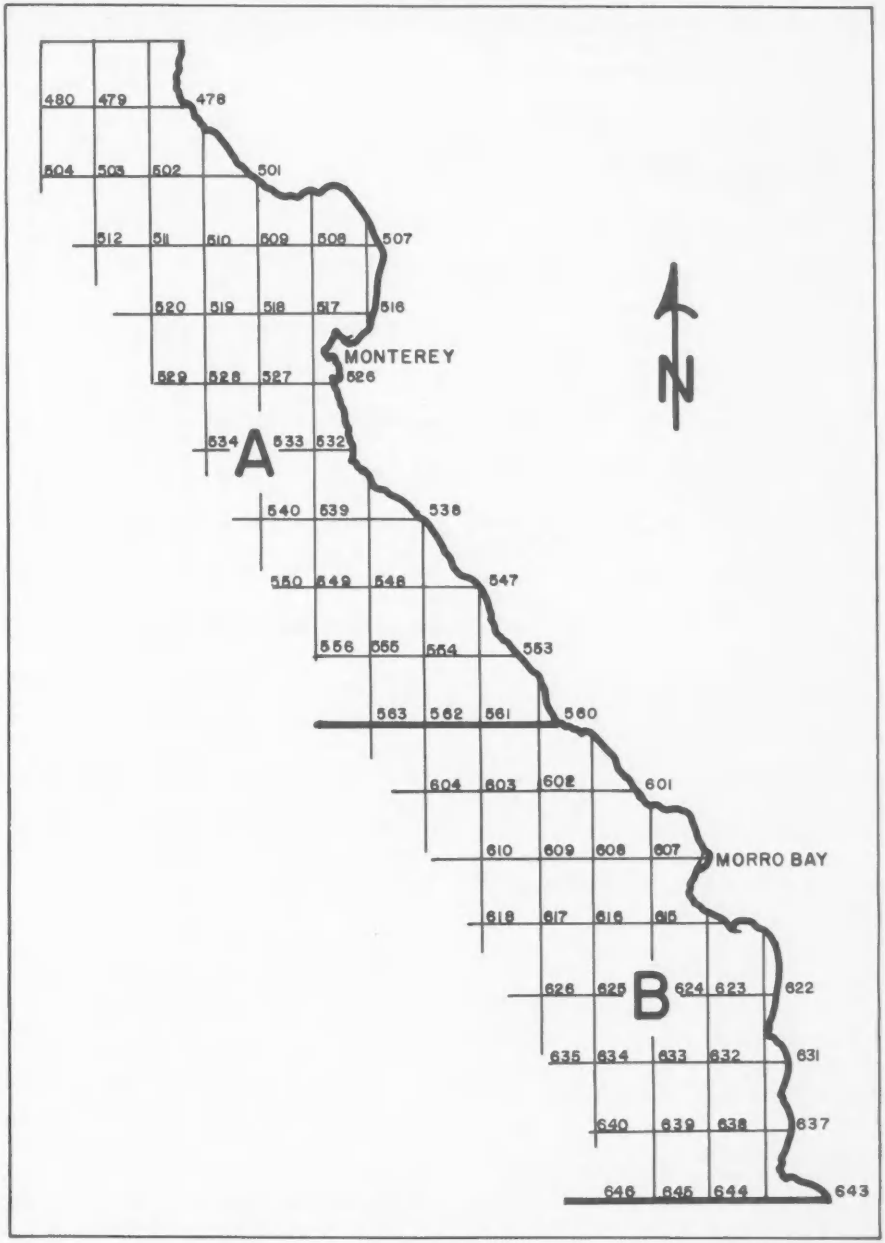

FIGURE 2.—Block areas grouped into zones (A-B), selected to outline the more important coastal fishing areas.

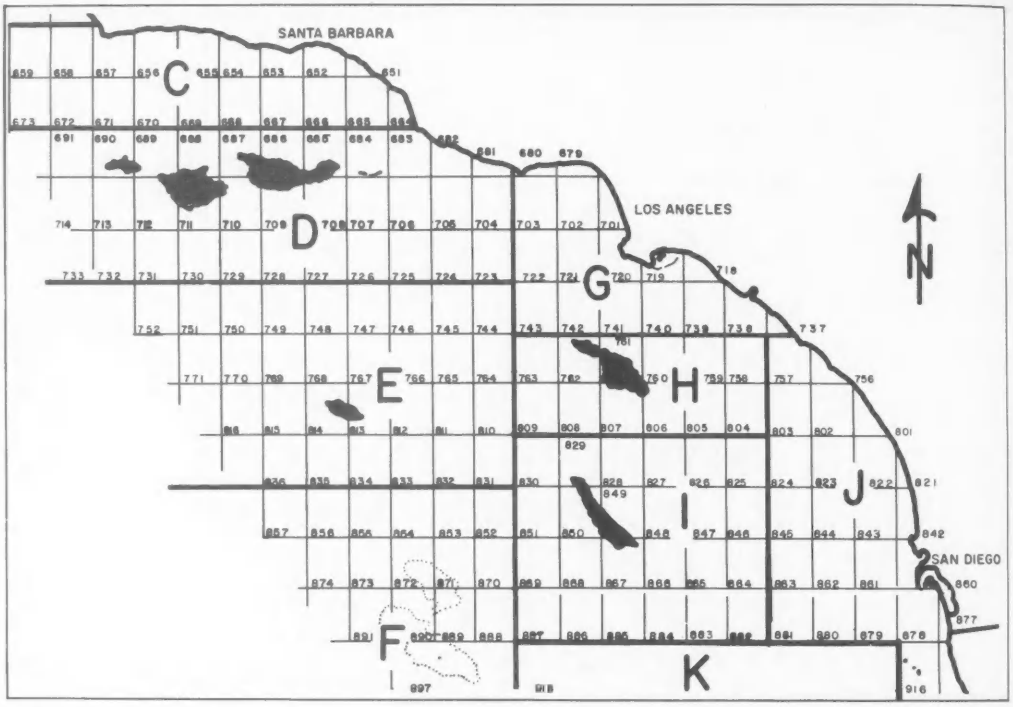

FIGURE 3.—Block areas grouped in zones (C-K), selected to outline the more important coastal fishing areas.

4. Whales, porpoises, and sharks were recorded as numbers of individuals observed.

5. When the flight track entered any portion of a block area, the block area was credited for the purpose of determining observation effort as having a "block area flight."

RESULTS

During survey flights, 20 species of fish were observed and identified. A number of other marine species (mammals, invertebrates) were observed and all are listed in Table 1.

DISTRIBUTION OF FLIGHT OBSERVATION EFFORT

A total of 17,593 flight hours were logged by spotter pilots during the survey period. The number of block area flights from September 1962 through the end of 1969 totaled 57,628 with 37,186 block areas surveyed during the day and 20,442 at night. Distribution of day and night block area flights by year and by zone is shown in Table 2.

NOCTURNAL AND DIURNAL VARIATION IN NUMBER OF SIGHTINGS AND TONNAGE

To determine criteria concerning the frequency of observation during the day and night for each of the species more commonly observed, the ratios in numbers of sightings and tonnages observed were calculated for the period September 1962 through December 1966. Information on the diurnal and nocturnal frequencies and magnitude of occurrence for each species is of importance in evaluating which observation (day

TABLE 1.—Species of fish and other marine animals observed during surveys.

Fish:
- Basking shark *(Cetorhinus maximus)*
- White shark *(Carcharodon carcharias)*
- Northern anchovy *(Engraulis mordax)*
- Pacific sardine *(Sardinops sagax)*
- Pacific bonito *(Sarda chiliensis)*
- Jack mackerel *(Trachurus symmetricus)*
- Pacific mackerel *(Scomber japonicus)*
- Pacific barracuda *(Sphyraena argentea)*
- Yellowtail *(Seriola dorsalis)*
- White seabass *(Cynoscion nobilis)*
- Bluefin tuna *(Thunnus thynnus)*
- Albacore tuna *(Thunnus alalunga)*
- Yellowfin tuna *(Thunnus albacares)*
- Skipjack tuna *(Katsuwonus pelamis)*
- Jacksmelt *(Atherinopsis californiensis)*
- Ocean sunfish *(Mola mola)*
- Striped bass *(Morone saxatilis)*
- Pacific saury *(Cololabis saira)*
- Swordfish *(Xiphias gladius)*
- Striped marlin *(Tetrapturus audax)*

Mammals:
- Gray whale
- Pilot whale
- Blackfish (killer whale)
- Porpoise and dolphin
- Seals and sea lions

Invertebrates:
- Squid
- Jellyfish

or night) might be the more significant in evaluating the trend of apparent abundance. These data were calculated during an earlier part of the study (1962-1966) to evaluate the method of using aerial fish spotter data.

The total amount of fish estimated to have been seen by the aerial fish spotters during the period 1962-1966 was 5,289,521 tons of the following species: northern anchovy, 4,550,218 tons; jack mackerel, 335,794 tons; Pacific bonito, 238,247 tons; Pacific mackerel, 103,464 tons; and yellowtail, 1,955 tons.

Annual sightings of each species per block area flight were expressed as a percentage of all block area flights day and night (% day/% night) and are shown in Table 3. The ratio of diurnal and nocturnal sightings was obtained by dividing the percentage of day sightings by the percentage of night sightings. Ratio values greater than 1.00 indicate a greater number of sightings during day, less than 1.00 indicate greater number of sightings during the night.

To determine the day and night differences in the tonnage observed for each species, the

TABLE 2.—Observation effort (day/night) in block area flights by zone for the period September 1962 through 1969. [Data are presented in number of block area flights (day/night).]

Zone	1962	1963	1964	1965	1966	1967	1968	1969	Total
A	41/62	175/78	125/86	102/84	239/9	361/0	585/0	86/29	1,714/348
B	174/117	220/75	283/156	471/252	770/90	610/13	519/0	126/10	3,173/713
C	104/126	470/658	632/680	892/743	1,860/495	1,016/559	1,014/281	2,130/718	8,118/4,260
D	12/71	137/167	409/518	485/434	1,268/385	813/533	1,000/291	1,942/712	6,066/3,111
E	0/10	63/96	40/263	48/58	108/30	40/51	101/109	87/97	493/714
F	0/6	15/32	23/37	2/106	37/21	15/53	35/194	79/48	206/497
G	0/2	454/496	394/610	481/404	1,358/434	874/596	616/676	735/1,500	4,939/4,718
H	0/0	291/282	363/336	387/349	723/206	435/305	368/469	303/576	2,870/2,523
I	0/0	366/155	477/157	395/258	814/208	614/281	544/378	613/348	3,823/1,785
J	0/0	463/198	586/300	550/128	847/113	1,087/154	672/294	932/188	5,137/1,375
K	0/0	18/0	13/0	13/0	69/9	65/10	75/32	106/1	350/52
Total	331/394	2,672/2,237	3,336/3,143	3,826/2,816	8,120/2,000	5,936/2,555	5,826/3,070	7,139/4,227	37,186/20,442
Grand total	725	4,909	6,479	6,642	10,120	8,491	8,896	11,366	57,628

TABLE 3.—Annual sightings per block area flight in percentage (day/night) and day/night averages and ratios.

Species	1962	1963	1964	1965	1966	Day/night	
						Average	Ratio
Northern anchovy	3.3/21.6	8.7/19.7	7.8/21.5	4.9/11.8	5.4/25.0	6.0/19.9	0.30
Pacific bonito	6.3/ 6.3	7.3/ 5.1	9.7/ 3.4	8.3/ 1.7	6.3/ 2.5	7.5/ 3.8	1.99
Jack mackerel	0.3/ 1.0	3.5/ 9.9	5.0/ 6.7	3.3/ 6.2	1.8/ 5.7	2.7/ 6.1	0.47
Pacific mackerel	0.0/ 6.9	4.2/ 9.6	2.0/ 3.5	0.3/ 1.2	0.1/ 2.0	1.3/ 4.6	0.28
Pacific sardine	1.2/ 1.5	1.5/ 2.3	0.8/ 2.1	0.1/ 0.4	0.2/ 0.4	0.7/ 1.3	0.57
Yellowtail	0.0/ 0.0	1.0/ 0.4	0.2/ 0.0	0.2/ 0.0	0.2/ 0.0	0.3/ 0.0	4.00
Pacific barracuda	1.8/ 0.0	0.9/ 0.6	0.5/ 0.6	0.7/ 0.0	0.2/ 0.1	0.8/ 0.2	3.15

amount observed (day or night) in each zone was divided by the number of block area flights (day or night) within the zone. The average number of tons observed per block area flight for each zone, the average number of tons observed for all zones combined, and ratios of day and night tonnages observed are shown in Table 4. Ratios were obtained by dividing the tons per block area flight (day) by tons per block area flight (night). Therefore, ratios greater than 1.00 indicate greater tonnage during the day, less than 1.00 indicate greater tonnage during the night.

AVERAGE WEIGHT OF FISH SCHOOLS

Average weight of schools was computed for the period September 1962 through December 1966 from all data having estimates of individual schools by weight. As previously indicated, some tonnages were given by areas, not by numbers of schools and tonnages of each school. The average tonnage per school is listed for each species in Table 5.

INDEX OF ANNUAL APPARENT ABUNDANCE

An index of annual apparent abundance was calculated for observations during day and night for each zone and for all zones combined from September 1962 through December 1969 for the northern anchovy, Pacific bonito, jack mackerel, Pacific mackerel, Pacific sardine, yellowtail, and Pacific barracuda. Marr (1951) defined the term apparent abundance as "abundance as affected by availability, or the absolute number of fish accessible to a fishery." This definition of apparent abundance most nearly describes the type of index calculated in this paper.

For convenience in calculating this index, four arbitrary tonnage ranges were selected for each species. Tonnage ranges for each species were selected to cover the entire range of observed tonnages that may occur in any one block area. The midpoint tonnage of each range was divided by 100 for the northern anchovy and by 10 for Pacific bonito, jack mackerel, Pacific mackerel, and Pacific sardine to provide a tonnage range value (X) of convenient size to be used in the

TABLE 4.—Day/night differences in tonnage and ratios observed based on average tons observed per block area flight in each zone for the period September 1962-1966.

Species and zone	Tons/block area flight day/night	Day/night ratio
Northern anchovy		
Zone A	478.8/636.1	0.75
B	148.5/832.2	0.17
C	45.4/386.4	0.11
D	32.6/337.5	0.09
E	9.8/214.0	0.04
F	3.9/ 39.2	0.01
G	105.0/197.3	0.53
H	64.4/ 75.8	0.84
I	10.8/ 92.3	0.11
J	32.6/237.1	0.13
K	13.5/ 11.1	1.21
Average—all zones	79.8/299.7	0.26
Pacific bonito		
Zone A	0.6/ 0.0	--
B	0.5/ 0.2	2.50
C	15.8/ 7.6	2.00
D	12.8/ 2.1	6.09
E	44.5/ 0.1	445.00
F	0.6/ 0.0	--
G	5.8/ 0.9	6.44
H	5.5/ 2.2	2.50
I	7.0/ 0.8	8.75
J	27.6/ 11.3	2.44
K	0.2/ 0.0	--
Average—all zones	10.9/ 2.3	4.73
Jack mackerel		
Zone A	41.7/ 12.2	3.48
B	25.3/ 44.8	0.56
C	2.5/ 6.0	0.41
D	9.2/ 34.6	0.27
E	2.5/ 19.2	0.13
F	8.0/169.4	0.04
G	2.3/ 6.1	0.37
H	1.7/ 8.2	0.20
I	5.8/ 17.0	0.34
J	4.0/ 11.5	0.34
K	0.0/ 0.0	--
Average—all zones	7.7/ 18.4	0.41
Pacific mackerel		
Zone A	0.0/ 0.0	--
B	0.0/ 1.1	0.00
C	0.8/ 5.7	0.14
D	2.5/ 3.8	0.65
E	0.5/ 6.4	0.07
F	50.1/ 50.3	0.99
G	2.0/ 2.0	1.00
H	11.1/ 5.9	1.88
I	1.7/ 2.4	0.70
J	2.7/ 8.4	0.32
K	3.2/ 0.0	--
Average—all zones	2.6/ 5.2	0.50
Pacific sardine		
Zone A	9.5/ 4.5	2.11
B	0.6/ 3.9	0.15
C	0.1/ 0.1	1.00
D	0.2/ 0.2	1.00
E	3.0/ 57.4	0.05
F	16.6/ 6.1	2.72
G	0.2/ 1.2	0.16
H	0.2/ 7.0	0.02
I	0.0/ 0.0	--
J	0.1/ 1.1	0.90
K	0.0/ 0.0	--
Average—all zones	0.7/ 4.1	0.17
Yellowtail	(Note, small number of observations, zone data omitted.)	
Average—all zones	0.09/0.02	4.50
Pacific barracuda	(Note, small number of observations, zone data omitted.)	
Average—all zones	0.06/0.29	0.20

TABLE 5.—Average weight per school (data from September 1962 through December 1966).

Species	Total tons / No. schools obs.	=	Avg. tons/school
Northern anchovy	192,047.5 / 5,261	=	36.5
Pacific sardine	5,140.5 / 194	=	26.5
Jack mackerel	44,545 / 1,846	=	24.1
Skipjack tuna	260 / 14	=	18.6
Albacore	73 / 4	=	18.2
Bluefin tuna	7,092 / 396	=	17.9
Pacific bonito	38,435 / 2,244	=	17.1
Pacific mackerel	10,948 / 649	=	16.9
Yellowtail	754.5 / 53	=	14.2
White seabass	234 / 47	=	4.9
Pacific barracuda	834.5 / 184	=	4.5

index formula. Midpoints were not reduced for Pacific barracuda and yellowtail. Range of observed tonnage and X values are shown in Table 6.

The following formula was used to calculate annual indexes of apparent abundance, day and night, for each species by zone and the day/night index of annual average apparent abundance for each species.

Index of apparent abundance

$$= \frac{\sum N_1X_1 + N_2X_2 + N_3X_3 + N_4X_4}{N_t}$$

where: $N_{1,2,3,4}$ = number of block area flights in which the species occurred at value $X_{1,2,3,4}$.
$X_{1,2,3,4}$ = tonnage range values.
N_t = total number of block area flights in the zone during the year.

Day and night indexes of apparent abundance for each zone and the annual average day/night indexes of apparent abundance for all zones are listed in Table 7.

DISCUSSION AND SUMMARY

A direct, precise measure of total abundance is most desirable for the management of pelagic marine species. However, at the present time and into the foreseeable future, this degree of accuracy in the measurement of total abundance cannot be attained. Therefore, pelagic resource mangement will be required to rely on an indirect measure of total abundance. Some observations on the relation between the index of apparent abundance and changes in estimates of total abundance can be made. For the years 1963 through 1969, either separately or combined, some data are available giving estimates of total abundance, spawning biomass, or indexes of abundance for such species as the northern anchovy, Pacific mackerel, Pacific sardine, jack mackerel, and Pacific bonito. However, all such estimates were calculated from data obtained from such measures as catch, effort, catch composition, fecundity, and egg and larval counts. No direct measurements of total abundance were

TABLE 6.—Range of tonnage and tonnage range values (X).

Species	Observed tonnage	X
Anchovy	0-400	2
	400-1,000	7
	1,000-10,000	55
	10,000-20,000	150
Pacific bonito	0-50	2.5
	50-150	10
	150-1,000	57.5
	1,000-5,000	300
Jack mackerel	0-50	2.5
	50-300	17.5
	300-1,000	65.5
	1,000-2,000	150
Pacific mackerel	0-20	1
	20-100	6
	100-250	17.6
	250-500	37.5
Pacific sardine	0-100	5
	100-500	30
	500-2,000	125
	2,000-4,000	300
Pacific barracuda	0-10	5
	10-30	20
	30-80	55
	80-160	120
Yellowtail	0-5	2.5
	5-10	7.5
	10-30	20
	30-60	45

TABLE 7.—Annual average indexes of apparent abundance for both day and night observations. Dash (__) indicates no flight observations in zone. Indexes given as day/night.

Zone	1962	1963	1964	1965	1966	1967	1968	1969
				Northern anchovy				
A	0.51/1.22	10.98/13.28	0.80/7.32	2.51/2.48	2.02/ 6.33	1.15/ __	0.28/ __	0.00/ 0.00
B	3.25/3.18	6.17/13.02	4.08/3.08	1.85/5.75	0.29/15.31	0.28/ 0.30	0.73/ __	0.03/ 0.00
C	0.05/0.99	0.40/ 2.70	0.90/2.85	1.82/8.63	0.27/ 2.79	2.91/ 3.03	0.05/ 1.76	0.87/ 1.93
D	0.00/2.97	1.24/10.02	0.23/4.75	0.48/3.67	0.14/ 6.73	0.63/ 5.12	0.05/ 3.24	0.41/ 1.96
E	__/0.00	0.00/ 1.05	0.00/3.14	0.00/0.12	1.09/ 0.23	3.15/ 0.11	0.18/ 0.12	0.32/ 0.67
F	__/0.00	3.66/ 1.71	5.75/0.37	0.00/0.58	0.00/ 2.61	0.00/ 0.00	0.00/ 0.60	0.00/ 0.00
G	__/1.00	0.51/ 1.81	0.54/6.21	1.42/3.23	2.24/ 1.78	2.40/ 8.32	0.55/ 2.11	5.01/ 8.57
H	__/__	0.14/ 0.12	0.38/1.00	0.05/1.90	2.28/ 1.43	5.45/ 1.60	0.65/ 0.58	6.35/ 3.26
I	__/__	0.14/ 0.00	0.05/0.11	0.02/0.34	0.28/ 2.53	2.87/ 0.71	0.18/ 0.21	0.78/ 0.49
J	__/__	0.78/ 0.67	0.85/6.08	0.00/0.00	0.45/ 1.55	0.16/20.16	0.52/ 1.11	0.55/ 3.39
K	__/__	0.00/ __	0.00/__	0.00/__	0.00/ 0.22	0.00/ 0.70	2.44/ 0.06	0.00/ 0.00
Average all zones	1.79/1.99	1.64/ 2.99	1.03/3.90	0.96/4.18	0.84/ 3.62	1.78/ 4.30	0.33/ 1.46	1.30/ 4.35
				Pacific bonito				
A	0.00/0.00	0.00/ 0.00	0.50/0.00	0.00/0.00	0.04/ 0.00	0.07/ __	0.00/ __	0.00/ 0.00
B	0.01/0.00	0.00/ 0.01	0.06/0.01	0.02/0.00	0.43/ 0.00	0.01/ 0.00	0.00/ __	0.00/ 0.00
C	0.62/0.25	3.63/ 1.51	2.40/0.82	2.18/0.40	1.38/ 0.83	0.51/ 1.02	0.36/ 1.36	0.29/ 0.27
D	0.83/0.63	0.65/ 1.88	1.40/0.12	0.85/0.10	1.27/ 0.54	0.38/ 0.80	0.53/ 0.15	0.24/ 0.23
E	__/0.00	0.02/ 1.15	0.50/0.00	6.81/0.00	4.30/ 0.00	0.00/ 0.00	0.00/ 0.02	0.00/ 0.00
F	__/0.00	0.00/ 0.00	0.43/0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	__/0.00	0.31/ 0.37	0.30/0.00	0.50/0.01	1.19/ 0.16	0.67/ 0.39	0.12/ 0.13	0.12/ 0.16
H	__/__	0.85/ 0.22	2.12/0.53	2.06/0.32	0.03/ 0.00	0.00/ 0.02	0.68/ 0.24	0.09/ 0.06
I	__/__	0.00/ 0.45	3.46/0.54	0.40/0.13	0.06/ 0.02	0.12/ 0.00	0.02/ 0.03	0.02/ 0.05
J	__/__	3.67/ 0.23	1.10/0.06	1.71/0.46	4.96/ 0.11	3.27/ 0.12	1.70/ 0.69	0.64/ 0.51
K	__/__	0.13/ __	0.00/__	0.00/__	0.00/ 0.00	45.73/ 0.00	0.26/ 0.00	0.75/ 0.00
Average all zones	0.23/0.19	1.62/ 0.58	1.62/0.28	1.26/0.19	1.34/ 0.35	1.35/ 0.34	0.43/ 0.35	0.26/ 0.18
				Jack mackerel				
A	0.00/0.08	1.81/ 0.00	8.32/2.89	0.78/ 1.67	4.29/25.72	0.81/ __	0.91/ __	0.03/ 0.00
B	0.02/0.00	3.48/ 1.37	6.65/6.67	1.03/ 1.22	0.74/ 8.78	0.78/ 1.34	0.70/ __	0.00/ 0.00
C	1.59/0.45	0.96/ 0.49	0.83/0.56	0.14/ 0.33	0.06/ 0.03	0.04/ 0.33	0.13/ 0.02	0.11/ 0.17
D	0.00/1.45	1.79/13.77	2.72/5.36	1.44/ 1.40	0.24/ 1.62	0.41/ 0.24	0.21/ 0.20	0.15/ 0.33
E	__/0.00	0.27/ 4.74	0.93/2.31	0.72/ 1.55	0.16/ 7.38	0.00/ 2.15	0.24/ 4.09	0.00/ 4.41
F	__/2.91	11.16/39.70	1.63/2.31	0.00/17.41	0.00/27.91	0.00/38.84	10.87/27.77	3.50/13.08
G	__/0.00	1.23/ 1.76	0.64/0.99	0.02/ 0.29	0.00/ 1.05	0.00/ 0.10	0.02/ 0.00	0.13/ 0.26
H	__/__	0.56/ 1.34	0.01/1.11	0.71/ 0.43	0.04/ 2.18	0.01/ 0.33	0.00/ 0.26	0.00/ 0.59
I	__/__	2.11/ 5.53	0.17/1.86	1.35/ 0.75	0.19/ 2.37	0.04/ 3.27	0.00/ 1.27	0.04/ 1.58
J	__/__	0.67/ 0.54	0.72/1.51	0.86/ 0.96	0.00/ 0.06	0.00/ 0.03	0.08/ 1.07	0.06/ 0.30
K	__/__	0.00/ __	0.00/__	0.00/ __	0.00/ 0.00	0.00/ 1.75	0.00/ 1.09	0.00/ 0.00
Average all zones	0.51/0.46	1.41/ 2.98	1.62/2.18	0.71/ 1.36	0.28/ 1.94	0.20/ 1.41	0.30/ 2.25	0.11/ 0.65
				Pacific mackerel				
A	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ __	0.00/ __	0.00/ 0.00
B	0.30/ 0.03	0.00/ 1.56	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ __	0.00/ 0.00
C	0.00/ 3.15	0.23/ 0.37	0.03/0.30	0.04/ 0.28	0.01/ 0.35	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
D	0.50/ 0.30	1.41/ 2.20	0.49/0.23	0.05/ 0.08	0.00/ 0.01	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
E	__/ 3.75	0.43/ 0.67	0.02/0.74	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.03	0.00/ 0.00
F	__/ 0.00	5.40/ 6.59	3.15/3.62	0.00/ 0.23	0.00/ 2.95	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	__/18.75	0.79/ 0.46	0.78/0.13	0.00/ 0.44	0.00/ 0.04	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
H	__/ __	2.19/ 1.62	0.14/0.36	0.00/ 0.02	0.00/ 0.02	0.00/ 0.00	0.00/ 0.00	0.00/ 0.03
I	__/ __	0.76/ 0.40	0.01/0.53	0.00/ 0.11	0.00/ 0.09	0.00/ 0.02	0.00/ 0.00	0.00/ 0.04
J	__/ __	0.83/ 1.44	0.75/0.29	0.00/ 0.36	0.00/ 0.06	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
K	__/ __	1.94/ __	0.00/__	0.00/ __	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
Average all zones	0.17/ 1.26	0.79/ 0.91	0.33/0.33	0.01/ 0.19	0.00/ 0.14	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00

TABLE 7.—Continued.

Zone	1962	1963	1964	1965	1966	1967	1968	1969
				Pacific sardine				
A	0.00/ 0.00	1.40/ 3.78	1.22/0.05	0.04/ 0.00	0.00/ 0.00	0.00/ --	0.00/ --	0.00/ 0.00
B	0.05/ 2.13	0.31/ 0.00	0.26/1.63	0.00/ 0.00	0.00/ 0.38	0.00/ 0.00	0.00/ --	0.00/ 0.00
C	0.04/ 0.00	0.02/ 0.00	0.00/0.05	0.07/ 0.02	0.00/ 0.00	0.00/ 0.03	0.00/ 0.00	0.00/ 0.00
D	0.00/ 0.28	0.07/ 2.36	0.23/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
E	--/12.50	2.22/ 0.83	1.75/7.87	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
F	--/ 0.00	0.00/ 0.00	13.47/1.62	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	--/ 0.00	0.08/ 0.30	0.17/0.13	0.03/ 0.00	0.00/ 0.09	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
H	--/--	0.06/ 0.67	0.00/2.27	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.02	0.00/ 0.00
I	--/--	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.02	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
J	--/--	0.12/ 0.05	0.22/0.01	0.00/ 1.09	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
K	--/--	0.00/ --	0.00/--	0.00/ --	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
Average all zones	0.04/ 1.00	0.22/ 0.50	0.27/1.03	0.02/ 0.05	0.00/ 0.04	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
				Pacific barracuda				
A	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ --	0.00/ --	0.00/ 0.00
B	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.24/ 0.00	0.00/ 0.00	0.00/ --	0.00/ 0.00
C	0.00/ 0.00	0.34/ 0.43	0.45/0.48	0.25/ 0.00	0.02/ 0.00	0.02/ 0.00	0.03/ 0.01	0.04/ 0.00
D	0.00/ 0.00	0.00/ 0.00	0.00/0.01	0.00/ 0.00	0.01/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
E	--/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
F	--/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	--/ 0.00	0.00/ 0.11	0.00/0.00	0.02/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
H	--/ --	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.11/ 0.00	0.00/ 0.00	0.00/ 0.00
I	--/ --	0.00/ 0.00	0.00/0.31	0.40/ 0.00	0.02/ 0.00	0.01/ 0.00	0.00/ 0.00	0.00/ 0.00
J	--/ --	0.15/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.04/ 0.00
K	--/ --	0.04/ --	0.00/--	0.00/ --	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
Average all zones	0.00/ 0.00	0.08/ 0.15	0.08/0.12	0.10/ 0.00	0.03/ 0.00	0.00/ 0.00	0.01/ 0.00	0.02/ 0.00
				Yellowtail				
A	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ --	0.00/ --	0.00/ 0.00
B	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.07/ 0.00	0.00/ 0.00	0.00/ --	0.00/ 0.00
C	0.00/ 0.00	0.03/ 0.04	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
D	0.00/ 0.00	0.36/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
E	--/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
F	--/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	--/ 0.00	0.00/ 0.00	0.00/0.00	0.01/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
H	--/ --	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
I	--/ --	0.55/ 0.64	0.13/0.04	0.34/ 0.07	0.39/ 0.00	0.09/ 0.00	0.00/ 0.00	0.00/ 0.00
J	--/ --	0.63/ 0.10	0.00/0.00	0.16/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
K	--/ --	0.00/ --	0.00/--	0.00/ --	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
Average all zones	0.00/ 0.00	0.19/ 0.06	0.01/0.00	0.06/ 0.00	0.04/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00

made which would provide a precise count of the population size.

From data for 1962 through 1966 the diurnal/nocturnal ratios in tonnage observed and in sightings indicate that the northern anchovy, jack mackerel, Pacific mackerel, and Pacific sardine were observed more frequently and in greater quantities at night. Pacific bonito and yellowtail were observed more frequently and in greater quantities during the day. However, Pacific barracuda were observed in greater quantity at night but more frequently during the day.

Indexes of apparent abundance for day and night observations and variations in total commercial catch (Lyles, 1963, 1964, 1965, 1966; Keilman and Allan, 1969) during the years 1963 through 1969 are shown in Figures 4 through 7. The records for 1962 were incomplete (program initiated in September 1962) and were not considered in the discussion of the index.

In consideration of the day/night ratios, the indexes reflect the following:

Pacific sardine (Figure 4)—The Pacific sardine is observed in greater quantity and more frequently during the night; therefore, the night index should provide a better measure of the sardine's apparent abundance. The night index declined from 0.50 in 1963 to an index of less

than 0.00 in 1969. Some positive index values of less than 0.005 will be recorded as 0.00.

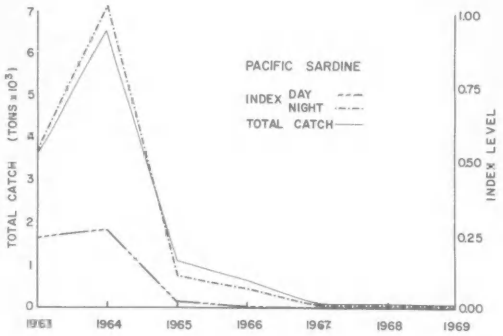

FIGURE 4.—Total catch and average index value for the Pacific sardine.

Pacific mackerel (Figure 5)—Data show that Pacific mackerel are observed in greater frequency and abundance during the night; therefore, the night index should be a better indicator of apparent abundance. The night index declined sharply from 0.91 in 1963 to 0.14 in 1966 and continued the decline to less than 0.00 in 1969.

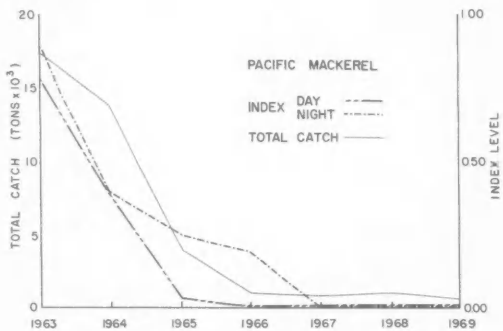

FIGURE 5.—Total catch, average index values for the Pacific mackerel.

Jack mackerel (Figure 6)—Observation of data show that jack mackerel is sighted more frequently and in greater abundance during the night; therefore, the night index should be the best measure of apparent abundance. The night index declined from 2.98 in 1963 to 1.36 in 1965; however, the index level showed an increase in 1968 to 2.25 and a sharp decline in 1969 to 0.65.

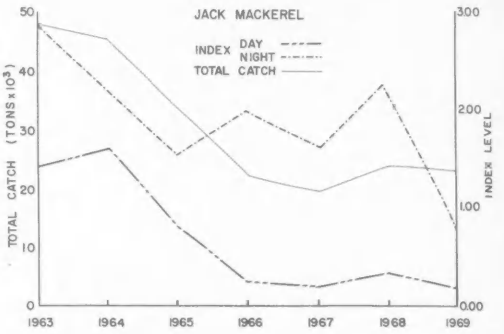

FIGURE 6.—Total catch and average index values for the jack mackerel.

Pacific bonito (Figure 7)—Bonito are observed in greater frequency and abundance during the day; therefore, the day index better represents any changes in apparent abundance. The day index showed only a slight decline during the 1963-1967 period, declining from 1.62 to 1.34. However, since 1967 the index has declined rapidly to a low in 1969 of 0.18.

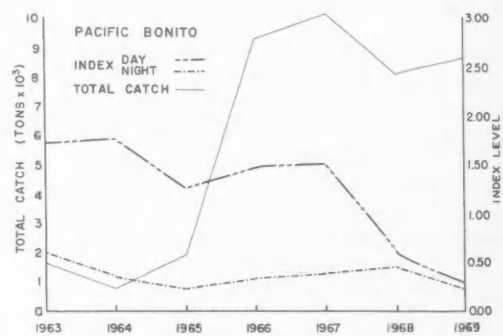

FIGURE 7.—Total catch and average index values for the Pacific bonito.

Northern anchovy (Figure 8)—Data indicate that the northern anchovy is observed more frequently and in abundance during the night; therefore, the night index should better reflect the apparent abundance of this species. The night index increased from 2.99 in 1963 to 4.30 in 1967, declined in 1968 to 1.46, and increased to a high level of 4.35 in 1969.

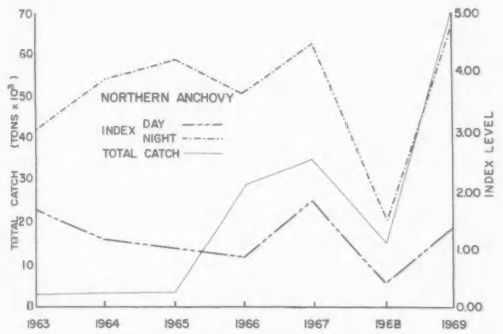

FIGURE 8.—Total catch and average index values for the northern anchovy.

Yellowtail and barracuda—Indexes have declined for both species (see Table 7); however, the frequency of observation was low, and no comparisons can be made with trends in abundance.

The relation between the trend of the apparent abundance index and of the trend of abundance estimates, where available, are discussed for the following species:

Pacific sardine—During the period 1963-1969, the Pacific sardine population continued to decline to a very low level, and the population is now at a fraction of that calculated for the 1930's and 1940's. Since no recent annual estimates are available (latest is 190,000 tons for 1959), a direct comparison of the estimates of total abundance with the index of apparent abundance cannot be made; however, the trend of the index follows closely the downward trend of the commercial catch.

Pacific mackerel—The Pacific mackerel fishery in southern California has been the subject of comprehensive research by the California Department of Fish and Game for many years. For purposes of comparison between trends of the index and population estimates, the more recent data for Pacific mackerel provides the best source of comparative statistics.

The Pacific mackerel catch has declined to a low level in recent years, and the trend of the index follows closely the catch decline (see Figure 5). Population estimates have been calculated by a number of workers. Blunt and Parrish (1969) summarized the knowledge of this fishery and reported estimates of total spawning biomass of 160 million pounds in 1963. Blunt[3] (personal communication) computed revised estimates for California waters using a modification of the Murphy method (Murphy, 1966). Revised figures indicate a spawning biomass of 64.5 thousand tons in 1962 and 78.5 thousand tons in 1963 reducing to less than 5,000 tons in 1968, an 84% or more, decline from 1963. The night index follows this 84% decline in estimated spawning biomass with an 89% index decline from 1.26 in 1963 to 0.14 in 1966 and to less than 0.00 in 1968.

Jack mackerel—Jack mackerel total abundance estimates are derived from egg and larval surveys. Ahlstrom (1968) estimated the adult spawning population in 1951-1954 for the California area to be between 1.4 and 2.4 million tons and that the resource was "much to moderately underutilized." In 1968 he estimated the population level to be approximately the same as was found in the earlier years.

The commercial fishery has experienced a substantial decline in catch over the past years and has extended its fishing grounds further offshore. Ahlstrom (1968) indicated the spawning population is centered in the oceanic waters. Blunt (1969) reported that in this offshore area the population is comprised of mature adults, some reaching the age of 30 years. The young fish remain inshore until 3 to 6 years old and then inhabit the offshore waters where they are outside the range of the normal fishery. The night aerial index shows a decline in apparent abun-

[3] C. E. Blunt, Jr., California Department of Fish and Game, Marine Resources Brancsh, 1416 Ninth St., Sacramento, CA 95814.

dance of these inshore younger fish, and this decline follows the downward catch trend.

Pacific bonito—The Pacific bonito has been abundant in southern California waters since the advent of the "warm years" of 1957-1958. Its northward latitudinal range into southern California waters is influenced by environmental conditions (Radovich, 1963). Figures on total abundance are not available. However, an index of abundance off southern California was developed from party boat catches by Radovich (1963). It is believed that party boat catches reflect the bonito's general abundance off southern California within certain limits. These limits were not defined and are due to the anglers preference for fishing more desirable species such as barracuda, yellowtail, albacore, etc., when they are available rather than fishing for bonito. Blunt (personal communication; see footnote 3) continued Radovich's study and calculated an index based on catch per angler day for the years 1962 through 1968. Values are as follows: 1962, (1.7), 1963 (1.5), 1964 (2.4), 1965 (1.4), 1966 (0.9), 1967 (0.6), 1968 (1.4). The highest party boat index level was in 1964. The index shows an increase for 1968 and differs from the index of apparent abundance; however, this index has shown an overall decrease since 1964.

The day index of apparent abundance shows an overall decrease from 1963 through 1969. The Pacific bonito is classed as "much underutilized" by Ahlstrom (1968). Due to economic factors and a decline in catches of jack and Pacific mackerel, the catch of bonito increased sharply in 1966 and 1967 with only a slight reduction in catch during 1968 and 1969. In contrast to this increase in catch level, the index of apparent abundance has shown a substantial decrease from 1.26 in 1965 to 0.26 in 1969. A considerable reduction in catch was experienced in 1970 (Lester A. Keilman, personal communication) as the total catch declined to 4,600 tons, about one-half the 1969 catch.

Northern anchovy—Studies by Ahlstrom (1968) estimated a total population of 1.8 to 2.3 million tons in 1958, increasing to 4.5 to 5.6 million tons in 1968. This estimate was based on data from larval counts and shows a population increase of approximately 8.6 times during the period 1951 through 1968. No total population estimates for the successive years 1963 through 1969 are available; however, Ahlstrom does state that the larval counts show that the population is somewhat variable from year to year and that the population reached a plateau in about 1962. Since annual abundance estimates are not available for the years 1963 through 1969, a direct comparison with the aerial spotter index cannot be made. The northern anchovy has increased substantially in abundance during the past decade and is classed as an underutilized species (Ahlstrom, 1968). Since it has been subjected only to minor fishery, except in 1969, it is generally agreed that the population level continued to be at high level throughout the years 1963-1969. The trend of the night aerial index of apparent abundance shows an overall increase during the years 1963 through 1969. The only significant change in apparent abundance was in 1968 when the index declined sharply; however, in 1969 it again increased to a high level.

Wide fluctuations in anchovy relative abundance were noted by Wood (1964, see footnote 2) during aerial surveys from 1956 to 1963. Future observations will determine if this paralleling of catch and apparent abundance will continue. Since the survey area covers an area common to the anchovy, trends in the annual index should be of use in evaluating catch variations and reflect the trend of total abundance in this underutilized resource.

In summary, for the geographical area normally surveyed by the aerial fish spotter, the author believes these data represent a reasonable index of apparent abundance. Like all other measures presently available, the true relation of the index of apparent abundance to total abundance for each species cannot be determined. However, from all data available concerning the Pacific mackerel, a species for which considerable and more reliable data on the adult population are available, the trend of the index follows the downward trend of the total abundance estimate. The index shows little effect from fluctuations in economic demand, as shown in data for the Pacific bonito. Trends in the abundance level of the Pacific bonito within the survey area are evident before they are reflected

in catches, and it appears to be a useful index in the evaluation of catch variations and long-term trends in total abundance in underutilized pelagic surface schooling resources.

ACKNOWLEDGMENTS

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The studies of Dr. Oscar E. Sette in the late 1940's must be recognized as one of the earliest applications of scientific aerial fish observations in the continuing search for new methods and techniques for obtaining abundance estimates of pelagic fishery resources.

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AN APPLICATION OF YIELD MODELS TO A CALIFORNIA OCEAN SHRIMP POPULATION

NORMAN J. ABRAMSON[1] AND PATRICK K. TOMLINSON[2]

ABSTRACT

Two types of yield models were utilized to analyze fishery data from California's northernmost bed of ocean shrimp, *Pandalus jordani*. The Schaefer form of stock production model was applied to catch and effort data for the years 1954 through 1969. Age-structured catch data for 1955 through 1968 were analyzed by the Murphy method to obtain mortality rates and biomass estimates. Catchability coefficients and a growth curve were also estimated. Attempts to fit spawner-recruit models to estimates obtained from the age-structured catch data were inconclusive; so, age specific mortality and growth estimates were only used to fit a yield-per-recruit model.

After comparing the results from the two models, the Schaefer model was deemed most suitable for managing this fishery. The model estimated the maximum sustainable yield at 2.46 million pounds. A strategy for managing the fishery under a quota system was proposed.

The fishery for ocean shrimp, *Pandalus jordani*, in California has a unique importance despite the fact that it does not rank high among the State's fisheries in terms of pounds landed or value of the landings. This unique importance exists since the fishery developed after discovery of the shrimp beds by the California Department of Fish and Game's exploratory fishing and because it has been under continuous quota control by the California Fish and Game Commission since the fishery's inception in 1952 (Dahlstrom 1961, 1970). It is also the only California commercial fishery whose catch is fully regulated under a quota system.

This paper is limited to a discussion of the population and fishery which range along the coast from the mouth of the Mad River in California to the Rogue River in Oregon. This fishery consists primarily of regulated California vessels, but there is a small Oregon fleet not covered by California's regulations while fishing north of the California border. Three smaller populations which occur farther south in California are not considered here.

Initially, quotas were set arbitrarily at one-fourth the estimated biomass on the bed. Biomass was originally estimated from an examination of commercial catch data and later from research vessel cruise data. In later years, quota recommendations were at least partially directed toward allowing what was deemed an appropriate spawning stock to remain at the end of the season. Spawning stock values were based on estimated preseason year class abundance and estimated survival over the fishing season.

Estimating procedures which assume commercial or research fishing gear catches all shrimp in the water column above the swept path must inherently be negatively biased since escapement over, around, and through the gear occurs. The methods just discussed are of this type. A more complete account of the basis for quota recommendations prior to 1969 is found in Dahlstrom (1961, 1970), Dahlstrom and Gotshall (1969), and Gotshall (in press).

Over the history of this fishery substantial amounts of data have been collected. Of relevance to this paper are catch and effort data, estimated age and sex composition of landings,

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and research vessel biomass estimates for 1965 through 1968. These data were used in applying a stock production model and a dynamic pool model. The general characteristics of these two models were discussed by Schaefer and Beverton (1963) under the designations of "Schaefer Approach" and "Beverton-Holt Approach," respectively.

STOCK PRODUCTION MODEL

From an operational viewpoint stock production models possess the advantage of requiring only catch and effort data, which are usually available at relatively little expense, for their fitting. Another desirable characteristic is the inclusion of density dependent effects, even though they are treated grossly and population response to density is assumed to be instantaneous. Pella and Tomlinson (1969) discuss the assumptions implicit in the model. The most notable fisheries application of this type model was to yellowfin tuna of the eastern Pacific by Schaefer (1954, 1957), who developed a method for fitting the model to a population in a non-equilibrium state.

Pella (1967) examined a number of methods for estimating parameters of the Schaefer model and concluded that a surface searching technique for minimizing the summed, squared deviations between observed catches and catches predicted by an integrated form of the Schaefer model was generally most satisfactory.

Pella and Tomlinson (1969) generalized the Schaefer model to allow asymmetry in the integrated form and gave the population growth rate as

$$\frac{dP(t)}{dt} = HP^m(t) - KP(t) - qf(t)P(t), \quad (1)$$

where H, K, m, and q are constants. $P(t)$ represents the population size at time t, $f(t)$ is the fishing intensity at t, q is the catchability coefficient, and m determines the amount of asymmetry in the equilibrium yield curve. In the Schaefer model, $m=2$ and the equilibrium curve is a parabola. The integral of (1) from time 0 to t with f constant is

$$P(t) = \left[\frac{H}{K+qf} - \left(\frac{H}{K+qf} - P(0)^{1-m}\right) \times e^{-(K+qf)(1-m)t}\right]^{\frac{1}{1-m}} \quad (2)$$

and Pella and Tomlinson (1969) used a numerical approximation of

$$C(t) = \int_0^t qf(t)P(t)\,dt \quad (3)$$

for computer calculation of expected catch over the interval. Pella (1967) gives the integrated form of (3) for the Schaefer model.

A computer program, GENPROD, (Pella and Tomlinson, 1969) for fitting the generalized model to catch and effort data uses the criterion of least squares between observed and predicted catches. Fox (1971) discusses least squares for estimating parameters in (2) and suggests alternatives which may be preferable to that used by GENPROD.

CATCH AND EFFORT DATA

Catch and effort data have been collected since the beginning of the fishery in 1952, but data from the first 2 years of the fishery are not used in this study because there was little effort and low catch-per-effort values indicated that fishermen had not fully acquired the skills needed for successfully catching shrimp. California landings were obtained from market receipts, and effort by California vessels was obtained from compulsory logbooks carried by all California trawlers. Oregon landings and effort were supplied by the Oregon Fish Commission (Jack Robinson, Oregon Fish Commission, personal communication).

California vessels were restricted to use of beam trawls until otter trawls became legal in 1963. Oregon vessels have used otter trawls since their entry into the fishery in 1960. A correction factor was used to convert California beam trawl effort to otter trawl effort for 1954 to 1962.

Fishing power of beam trawls relative to otter trawls was estimated from 40 pairs of catch-per-hour statistics. These paired statistics consisted of the average weekly catch-per-hour for

each gear within a 10-fm depth interval bounded by a 10-min by 10-min block area. The data were collected during 1960 through 1962 when Oregon vessels were using otter trawls and California vessels were still restricted to beam trawls. California Department of Fish and Game trawler logbooks and information supplied by the Oregon Fish Commission were the sources of the records (Tom Jow, California Department of Fish and Game, personal communication).

With otter trawl taken as the standard gear, the relative log fishing power of beam trawls was computed by Robson's (1966) method except the two gear types were used in a manner analogous to his treatment of individual vessels. If the logarithm of catch-per-hour is normally distributed and the other assumptions of Robson's model hold, then his method produces B_i, an unbiased estimate of relative log fishing power, β_i, for the ith gear. However, exp (B_i) is a biased estimate of exp (β_i). An unbiased estimator for exp (β_i) is given by Laurent (1963) as

$$\widehat{\exp(\beta_i)} = \left[\exp(B_i)\right]\left[1 + \sum_{j=1}^{\infty} \frac{(-1)^j}{j!2^j} \times \frac{(n-k-1)^j \left[v(B_i)\right]^j}{(n-k-1)(n-k+1)\ldots(n-k+2j-3)}\right], \quad (4)$$

where $v(B_i)$ is an unbiased estimate of the variance of B_i with $n-k-1$ degrees of freedom. Robson's method provides $v(B_i)$ and our computer program for calculating fishing power carries the series expansion in (4) to 15 terms. This computer program is described by Berude and Abramson (1972) and a FORTRAN listing is contained in Abramson (1971).

The estimated fishing power of beam trawls relative to otter trawls in the shrimp fishery was 0.71; all beam trawl effort used in this study was adjusted by that factor.

FITTING THE PRODUCTION MODEL

Usable catch and effort data covered a period of 16 years, each divided into open and closed seasons. Each season was treated as a separate interval in the fitting procedure and thus population estimates were obtained at 32 points in time. Table 1 shows catch, adjusted effort, and time for the series of seasons used to fit the generalized production model.

When initially fitting GENPROD to the data the parameters representing optimum effort (F_{opt}), catchability coefficient (q), maximum catch-per-effort (U_{max}), and the ratio of initial population to maximum population (r) were unrestricted. Pella and Tomlinson (1969) give these parameters as transformations of those in (2). The equation was fitted with the parameter m taking values from 1.4 to 2.6 by increments of 0.2. Results showed that number or distribution of data points was not sufficient to determine the value of m with any degree of precision and that very small population estimates accompanied by excessively large q values were being obtained.

The first problem was handled by setting $m = 2$, since the symmetric or Schaefer model seemed best in face of the uncertainty. The catchability coefficient was fixed at a value which minimized the sum of the squared deviations between GENPROD'S estimates of $P(t)$ and research vessel cruise estimates of population biomass at seven time points when both were available. The research vessel biomass estimates were obtained from surveys conducted in the spring and fall of 1965, 1966, and 1967 and the fall of 1968 (Gotshall, in press). Gotshall's catch in weight per standard haul was expanded on an areal basis to provide estimates for the entire survey area; as mentioned previously, these are negatively biased. Based on this procedure, $q = 8.5 \times 10^{-5}$ was the best value. The final fit of the Schaefer model was made with GENPROD's computing parameters KK and N set equal to 5 and 10, respectively. KK is related to the fineness of the surface searching procedure, and N involves the accuracy of the numerical integration used to estimate expected catch. These computing parameters are explained fully in Pella and Tomlinson (1969).

GENPROD estimated a maximum equilibrium catch (C_{max}) of 2.46 million pounds, an effort level required to obtain this catch under equilibrium conditions (F_{opt}) of 6,049 otter trawl

TABLE 1.—Estimates of Schaefer model parameters, observed catch and effort, predicted population size and catch, population and catch in millions of pounds, effort in thousands of hours.

Time interval		Population size end of interval	Applied effort	Observed catch	Predicted catch	Catch/effort	
Begin	End					Observed	Predicted
May 54	Aug. 54	8.63	0.206	0.169	0.150	0.819	0.727
Sept. 54	Apr. 55	9.07	0.0	0.0	0.0		
May 55	Oct. 55	8.82	0.733	0.505	0.557	0.689	0.760
Nov. 55	Apr. 56	9.11	0.0	0.0	0.0		
May 56	Sept. 56	8.57	1.11	0.896	0.836	0.803	0.750
Oct. 56	Apr. 57	9.00	0.0	0.0	0.0		
May 57	Oct. 57	8.59	1.05	0.748	0.783	0.713	0.746
Nov. 57	Apr. 58	8.96	0.0	0.0	0.0		
May 58	Sept. 58	8.18	1.61	1.14	1.17	0.706	0.726
Oct. 58	Apr. 59	8.76	0.0	0.0	0.0		
May 59	Sept. 59	7.83	2.01	1.69	1.41	0.841	0.702
Oct. 59	Mar. 60	8.45	0.0	0.0	0.0		
Apr. 60	Oct. 60	7.36	2.90	1.80	1.93	0.623	0.667
Nov. 60	May 61	8.22	0.0	0.0	0.0		
Jun. 61	Nov. 61	7.75	1.70	1.46	1.15	0.859	0.677
Dec. 61	Mar. 62	8.21	0.0	0.0	0.0		
Apr. 62	Oct. 62	6.39	4.70	2.98	2.87	0.635	0.611
Nov. 62	Mar. 63	7.23	0.0	0.0	0.0		
Apr. 63	Oct. 63	5.82	4.85	2.30	2.66	0.475	0.549
Nov. 63	Apr. 64	6.91	0.0	0.0	0.0		
May 64	Oct. 64	6.63	2.28	1.20	1.31	0.525	0.575
Nov. 64	Apr. 65	7.56	0.0	0.0	0.0		
May 65	Oct. 65	6.17	4.14	1.62	2.39	0.392	0.578
Nov. 65	Apr. 66	7.20	0.0	0.0	0.0		
May 66	Oct. 66	6.13	3.76	1.61	2.12	0.427	0.563
Nov. 66	Feb. 67	6.85	0.0	0.0	0.0		
Mar. 67	Oct. 67	6.22	3.71	2.26	2.05	0.608	0.553
Nov. 67	Apr. 68	7.24	0.0	0.0	0.0		
May 68	Oct. 68	6.72	2.54	2.67	1.50	1.052	0.592
Nov. 68	Feb. 69	7.36	0.0	0.0	0.0		
Mar. 69	Oct. 69	6.03	4.82	3.11	2.71	0.644	0.563
Nov. 69	Apr. 70	7.09	0.0	0.0	0.0		

Parameter estimates

C_{max}	F_{opt}	P_{opt}	q	U_{opt}	U_{max}	r	P_{max}	H	K
2.46	6.05	4.79	8.5×10^{-5}	0.407	0.814	0.884	9.58	-1.07×10^{-7}	−1.03

hours, and an optimum population size (P_{opt}) of 4.79 million pounds. Other parameter estimates, as defined by Pella and Tomlinson, and the complete output from the program are shown in Table 1.

Figure 1 shows both the expected catch as predicted by the model and the observed catch plotted against time. The fit appears to be generally quite good, although it has worsened during the most recent 5 years. The statistic R, derived by Pella and Tomlinson to measure the improvement in estimating catch from this model rather than from the mean catch, was 0.91. However, a somewhat spurious R is obtained when intervals with no catch are included in the data. This occurs because the model always predicts a zero catch from zero effort and the arithmetic mean cannot make such a prediction. Recalculating R from only periods when effort was applied yielded 0.75.

Figure 2 shows the fitted line ($m = 2$) for catch per unit effort versus effort in the equilibrium state and the observed catches per hour by year. However, the population should not

have been in equilibrium during the period studied since the level of effort fluctuated from year to year.

The actual catch exceeded the estimated maximum equilibrium yield (2.46 million pounds)

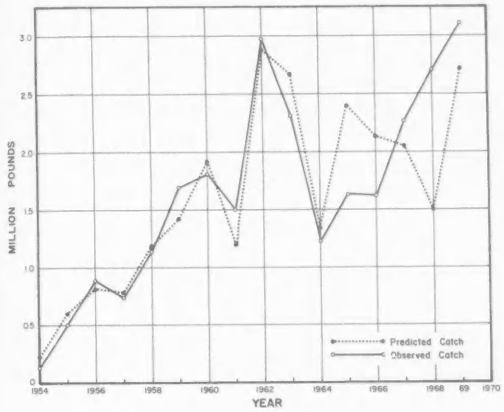

FIGURE 1.—Ocean shrimp catches predicted by GENPROD and observed catches for the years 1954 through 1969.

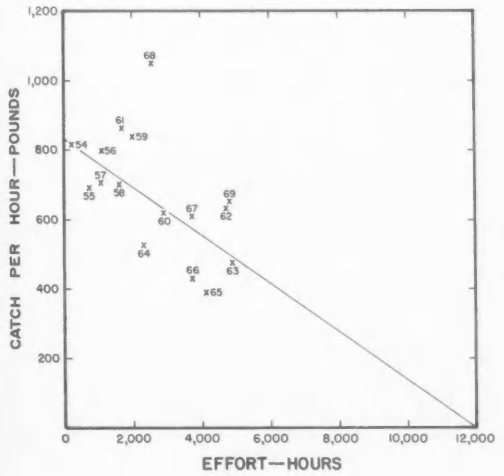

FIGURE 2.—Fitted model ($m = 2$) for catch-per-hour as a function of hours under equilibrium conditions.

during the period 1954 through 1969 only three times (Table 1): 1962, 1968, and 1969. Effort has always been substantially below the estimated level which would produce the maximum sustainable yield. A literal interpretation of these results would indicate the population has been underexploited until recently.

It is a problem in actual management situations to deduce how well a model such as this represents a population. In years when the observed catch-per-unit effort deviates substantially from the corresponding expected value, it cannot be determined whether deviations are due to an actual departure from the expected population size or due to a temporary change in the catchability. In the management strategy which we will discuss later, we are assuming the population size is being predicted correctly by the model and we are essentially ignoring deviations between the observed and expected catch insofar as they may represent actual population deviations.

DYNAMIC POOL MODEL

Catch data by age categories, both in weight and numbers, were utilized to estimate mortality, growth, and recruitment parameters necessary in a dynamic pool model.

AGE-STRUCTURED CATCH DATA

Catches from the population were landed at Eureka and Crescent City, Calif., and Brookings, Oreg. Landings data were obtained mainly from the Pacific Marine Fisheries Commission Data Series (1965-1969). Catches south of the California-Oregon border were recorded in that publication in tables for PMFC Area 96, but those from north of the border were included in, but did not comprise all of, the catch reported from PMFC Area 88. Catches within PMFC Area 88 south of the Rogue River were obtained from the Oregon Fish Commission (Jack Robinson, Oregon Fish Commission, personal communication). Catches made in the more recent years were obtained from the California Department of Fish and Game Shellfish Program (Daniel Gotshall and Walter Dahlstrom, California

Department of Fish and Game, personal communication). Virtually all catches were made during single day trips.

Landings were stratified into port-months, with Eureka-Crescent City as "California" and Brookings as "Oregon." Relative age frequency and weight at age were determined from samples of most port-month catches. Values used for California strata not sampled were either the average of preceding and following strata or the nearest sampled strata of the same season. The Oregon Fish Commission provided values for all Oregon strata.

Several methods of drawing samples from within strata were used by California. For all but very recent years, the methods were equivalent to assuming a simple random sample of shrimp from within strata. These sampled shrimp were aged by carapace length measurements, and the fraction falling into a specific age group determined its relative frequency. In recent years a simple random sample of boatloads was assumed drawn, and the length composition of a subsample from each boatload was weighted by the estimated number of shrimp in the load. Estimates by strata, done separately for Oregon and California, were combined to obtain the values in Table 2.

The average weight at age was determined by two methods: (1) the aged shrimp were placed into length frequency groups, a length-weight key was used to convert length to weight, and average weight for each age group was calculated; (2) the aged shrimp were weighed and an average weight computed directly for each age group. The study of aged catch data was performed for the 1955 through 1968 seasons. All aged shrimp fell into age groups 0, I, II, or III, but the 0 group was rare and omitted from the study.

Catch by age category for 2,598 million shrimp (22.88 million pounds) harvested during 1955 through 1968 are listed by month in Table 2. During the first 7 of these years, the fishery was active during 39 months and captured an estimated 954 million shrimp, excluding age 0, yielding a monthly average of 24.5 million. These shrimp weighed about 8.25 million pounds, averaging 212,000 lb. per month of fishing and 0.0086 lb. per shrimp. The fishery was active during 46 months of the second 7 years and caught an estimated 1,644 million shrimp, excluding age 0, for a monthly average of 35.7 million. These weighed about 14.63 million pounds, averaging 318,000 lb. per month and 0.0089 lb. per shrimp. The relative frequencies in numbers during the first 7 years were: 0.559 for age I, 0.422 for age II, and 0.019 for age III. During the second 7 years the frequencies were 0.495 for age I, 0.463 for age II, and 0.042 for age III. The reliability of the age frequency values is uncertain due to the aging method.

GROWTH CURVE

A growth in weight curve was obtained empirically by plotting average weights of shrimp by month and age for all seasons 1955 through 1968 (Tables 2 and 3, Figure 3). Dahlstrom (1970) and Gotshall (California Department of

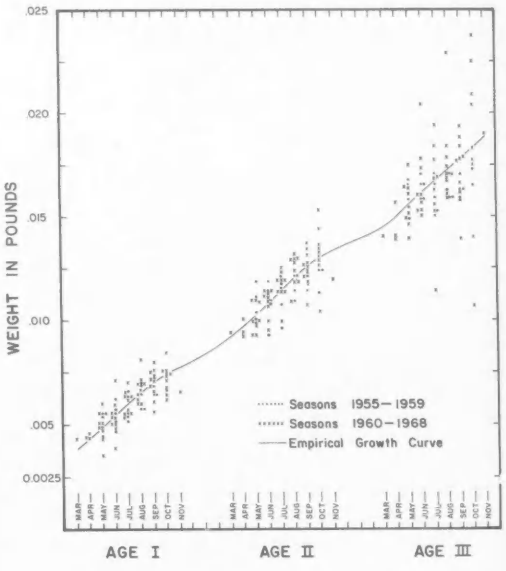

FIGURE 3.—Ocean shrimp growth in weight by month from sampling commercial landings. Seasons included are 1955 through 1968.

TABLE 2.—Aged catch[1] and catch-per effort (C.P.E.) statistics.
[Pounds and numbers in thousands.]

Season	Month	Age group	Relative frequency	Average weight (lb.)	C.P.E. numbers	Pounds	Numbers
1955	May	I	0.226	0.0055	9.9	4.3	782
		II	.747	.0118	32.7	30.4	2586
		III	.027	.0169	1.2	1.6	93
	June	I	.408	.0046	26.2	21.0	4531
		II	.576	.0118	37.0	75.3	6397
		III	.016	.0172	1.0	3.1	178
	July	I	.425	.0055	38.4	30.8	5603
		II	.565	.0122	51.0	90.8	7449
		III	.010	.0172	.9	2.3	132
	Aug.	I	.378	.0057	28.8	28.0	4897
		II	.603	.0122	46.0	95.3	7812
		III	.019	.0172	1.4	4.2	246
	Sept.	I	.588	.0064	49.9	47.7	7441
		II	.397	.0123	33.7	62.0	5024
		III	.015	.0172	1.3	3.3	190
	Oct.	I	.588	.0067	19.3	2.1	309
		II	.397	.0125	13.0	2.6	208
		III	.015	.0175	.5	.1	8
1956	May	I	.342	.0044	45.2	19.7	4479
		II	.608	.0099	80.4	78.8	7963
		III	.050	.0156	6.6	10.2	655
	June	I	.140	.0051	13.1	16.1	3166
		II	.833	.0093	78.2	174.4	18839
		III	.027	.0159	2.5	9.7	611
	July	I	.140	.0051	13.0	13.7	2697
		II	.843	.0097	78.5	157.7	16240
		III	.017	.0154	1.6	5.0	327
	Aug.	I	.161	.0057	13.0	27.8	4857
		II	.818	.0110	66.0	271.2	24680
		III	.021	.0169	1.7	10.7	634
	Sept.	I	.230	.0064	11.4	14.2	2221
		II	.753	.0115	37.3	83.6	7271
		III	.017	.0164	.8	2.7	164
1957	May	I	.366	.0053	29.5	22.0	4159
		II	.629	.0104	50.7	74.4	7147
		III	.005	.0167	.4	.9	57
	June	I	.592	.0057	33.4	21.9	3807
		II	.403	.0110	22.7	28.5	2592
		III	.005	.0167	.3	.5	32
	July	I	.592	.0063	33.0	11.2	1785
		II	.403	.0116	22.5	14.1	1215
		III	.005	.0167	.3	.3	15
	Aug.	I	.652	.0070	60.9	229.0	32515
		II	.343	.0122	32.0	208.6	17105
		III	.005	.0161	.5	4.0	249
	Sept.	I	.597	.0072	40.0	52.4	7235
		II	.386	.0122	25.8	57.0	4678
		III	.017	.0161	1.1	3.3	206
	Oct.	I	.597	.0074	50.9	9.0	1221
		II	.386	.0125	32.9	9.9	790
		III	.017	.0167	1.4	.6	35
1958	May	I	.429	.0048	30.1	41.6	8648
		II	.541	.0101	38.0	110.0	10906
		III	.030	.0150	2.1	9.1	605
	June	I	.429	.0055	37.2	82.3	14987
		II	.541	.0108	46.9	203.2	18899
		III	.030	.0159	2.6	16.6	1048
1958	July	I	.492	0.0053	29.7	30.9	5842
		II	.496	.0108	29.9	63.3	5890
		III	.012	.0152	.7	2.2	142
	Aug.	I	.596	.0064	64.8	121.7	18992
		II	.394	.0115	42.9	144.3	12555
		III	.010	.0161	1.1	5.1	319
	Sept.	I	.786	.0068	70.8	209.9	30849
		II	.209	.0118	18.8	95.9	8150
		III	.005	.0159	.5	3.1	195
1959	May	I	.599	.0055	87.2	104.0	18919
		II	.355	.0112	51.7	126.0	11213
		III	.046	.0159	6.7	23.1	1453
	June	I	.748	.0062	87.8	268.8	43542
		II	.240	.0115	28.2	160.6	13971
		III	.012	.0167	1.4	11.6	699
	July	I	.595	.0066	53.1	211.4	31921
		II	.382	.0118	34.1	241.1	20494
		III	.023	.0161	2.1	19.9	1234
	Aug.	I	.648	.0069	47.9	91.1	13120
		II	.329	.0120	24.3	80.3	6661
		III	.023	.0164	1.7	7.5	466
	Sept.	I	.720	.0073	66.8	207.3	28403
		II	.258	.0123	23.9	125.7	10178
		III	.022	.0164	2.0	14.2	868
1960	May	I	.601	.0042	45.1	48.2	11464
		II	.382	.0100	28.7	73.2	7287
		III	.017	.0153	1.3	5.0	324
	June	I	.689	.0050	53.2	94.0	18882
		II	.289	.0115	22.3	91.5	7920
		III	.022	.0162	1.7	9.8	603
	July	I	.798	.0055	78.5	321.7	58428
		II	.192	.0114	18.9	160.5	14058
		III	.010	.0172	1.0	12.6	732
	Aug.	I	.700	.0060	63.4	281.4	47073
		II	.276	.0110	25.0	204.0	18560
		III	.024	.0162	2.2	26.1	1614
	Sept.	I	.699	.0066	53.5	210.6	31760
		II	.264	.0122	20.2	146.6	11995
		III	.037	.0168	2.8	28.3	1681
	Oct.	I	.698	.0076	33.3	51.3	6790
		II	.280	.0132	13.4	35.9	2724
		III	.022	.0179	1.0	3.8	214
1961	June	I	.454	.0052	48.8	52.3	10053
		II	.531	.0112	57.1	131.5	11759
		III	.015	.0162	1.6	5.4	332
	July	I	.441	.0063	36.1	79.0	12559
		II	.549	.0126	44.9	196.7	15635
		III	.010	.0170	.8	4.8	285
	Aug.	I	.337	.0069	25.8	118.9	17195
		II	.643	.0131	49.2	428.3	32809
		III	.020	.0172	1.5	17.6	1021
	Sept.	I	.400	.0076	31.6	62.0	8152
		II	.574	.0135	45.3	158.1	11698
		III	.026	.0190	2.1	10.1	530
	Oct.	I	.222	.0073	15.7	23.4	3181
		II	.758	.0146	53.5	158.5	10860
		III	.020	.0227	1.4	6.5	287

TABLE 2.—Continued.

Season	Month	Age group	Relative frequency	Average weight (lb.)	C.P.E. numbers	Pounds	Numbers
1961	Nov.	I	.633	0.0066	33.1	4.8	728
		II	.345	.0121	18.0	4.8	397
		III	.022	.0192	1.2	.5	25
1962	Apr.	I	.460	.0043	38.6	44.8	10512
		II	.465	.0093	39.1	99.0	10626
		III	.075	.0141	6.3	24.1	1714
	May	I	.460	.0047	41.8	121.8	25684
		II	.465	.0100	42.3	259.1	25964
		III	.075	.0148	6.8	62.0	4188
	June	I	.460	.0050	30.9	80.2	15998
		II	.465	.0113	31.2	182.9	16172
		III	.075	.0180	5.0	46.8	2608
	July	I	.414	.0053	22.4	86.4	16208
		II	.537	.0120	29.0	253.3	21024
		III	.049	.0179	2.6	34.3	1918
	Aug.	I	.560	.0059	32.6	249.2	42011
		II	.395	.0129	23.0	382.9	29633
		III	.045	.0231	2.6	78.0	3376
	Sept.	I	.560	.0068	41.2	281.6	41305
		II	.410	.0128	30.2	387.7	30241
		III	.030	.0180	2.2	39.7	2213
	Oct.	I	.550	.0064	51.3	95.1	14976
		II	.380	.0136	35.4	140.8	10347
		III	.070	.0177	6.5	33.7	1906
1963	Apr.	I	.160	.0043	11.2	7.5	1751
		II	.770	.0094	54.0	79.3	8427
		III	.070	.0142	4.9	10.9	766
	May	I	.162	.0034	10.6	20.7	6028
		II	.750	.0092	49.0	257.7	27909
		III	.088	.0177	5.7	57.9	3275
	June	I	.171	.0038	8.9	26.1	6811
		II	.730	.0096	37.9	280.4	29077
		III	.099	.0155	5.1	61.1	3943
1963	July	I	.165	.0055	6.8	39.5	7236
		II	.725	.0114	29.7	361.7	31796
		III	.110	.0154	4.5	74.4	4824
	Aug.	I	.274	.0061	11.1	99.6	16226
		II	.674	.0125	27.3	497.1	39915
		III	.052	.0176	2.1	54.1	3079
	Sept.	I	.289	.0061	12.5	46.8	7687
		II	.661	.0119	28.7	209.3	17582
		III	.050	.0163	2.2	21.7	1330
	Oct.	I	.330	.0068	14.4	20.1	2943
		II	.660	.0127	28.9	74.8	5886
		III	.010	.0108	.4	1.0	89
1964	May	I	.460	.0059	26.4	65.6	11102
		II	.523	.0110	30.1	139.3	12622
		III	.017	.0165	1.0	6.8	410
	June	I	.430	.0071	23.5	95.2	13352
		II	.550	.0107	30.0	182.3	17078
		III	.020	.0206	1.1	12.8	621
	July	I	.505	.0069	24.1	68.8	9924
		II	.474	.0124	22.6	115.9	9315
		III	.021	.0196	1.0	8.1	413
	Aug.	I	.548	.0081	30.4	183.7	22554
		II	.431	.0132	23.9	233.4	17739
		III	.021	.0186	1.2	16.0	864
1964	Sept.	I	.548	0.0071	29.5	9.7	1359
		II	.431	.0128	23.2	13.7	1069
		III	.021	.0179	1.1	.9	52
	Oct.	I	.548	.0076	26.7	17.8	2351
		II	.431	.0131	21.0	24.3	1849
		III	.021	.0186	1.0	1.7	90
1965	May	I	.612	.0049	29.4	98.2	20029
		II	.275	.0098	13.2	88.4	9000
		III	.113	.0141	5.4	52.3	3698
	June	I	.704	.0048	47.7	168.8	35439
		II	.266	.0109	18.0	146.3	13390
		III	.030	.0154	2.0	23.3	1510
	July	I	.868	.0056	61.5	456.1	81360
		II	.119	.0115	8.4	128.8	11154
		III	.013	.0164	.9	19.9	1219
	Aug.	I	.858	.0069	35.6	177.7	25734
		II	.126	.0130	5.2	49.1	3779
		III	.016	.0172	.7	8.2	480
	Sept.	I	.865	.0075	30.9	105.2	14112
		II	.124	.0132	4.4	26.7	2023
		III	.011	.0185	.4	3.3	179
	Oct.	I	.807	.0074	30.6	48.7	6545
		II	.176	.0137	6.7	19.5	1427
		III	.017	.0211	.6	2.9	138
1966	May	I	.147	.0050	7.2	11.4	2273
		II	.795	.0093	38.9	114.4	12295
		III	.058	.0151	2.8	13.5	897
	June	I	.230	.0053	11.1	70.7	13397
		II	.735	.0100	35.6	426.8	42812
		III	.035	.0158	1.7	32.2	2039
	July	I	.252	.0062	13.4	94.5	15364
		II	.717	.0100	38.1	437.6	43714
		III	.031	.0116	1.6	22.0	1890
	Aug.	I	.292	.0064	9.9	33.4	5223
		II	.687	.0119	23.3	146.1	12289
		III	.021	.0161	.7	6.1	376
	Sept.	I	.410	.0072	12.6	36.1	5022
		II	.586	.0127	18.0	91.4	7178
		III	.004	.0181	.1	.9	49
	Oct.	I	.424	.0072	15.8	19.4	2682
		II	.567	.0134	21.1	47.9	3587
		III	.009	.0206	.3	1.2	57
1967	Mar.	I	.674	.0042	51.7	10.4	2482
		II	.159	.0094	12.2	5.5	586
		III	.167	.0142	12.8	8.7	615
	Apr.	I	.730	.0044	60.7	45.6	10444
		II	.176	.0101	14.6	25.5	2518
		III	.094	.0158	7.8	21.2	1345
	May	I	.723	.0048	47.3	11.9	2461
		II	.176	.0110	11.5	6.6	599
		III	.101	.0162	6.6	5.6	344
	June	I	.739	.0055	61.8	294.7	53862
		II	.225	.0115	18.8	188.9	16399
		III	.036	.0152	3.0	39.8	2624
	July	I	.804	.0063	79.0	672.5	106859
		II	.172	.0120	16.9	273.3	22860
		III	.024	.0157	2.4	50.2	3190

TABLE 2.—Continued.

Season	Month	Age group	Relative frequency	Average weight (lb.)	C.P.E. numbers	Pounds	Numbers
1967	Aug.	I	.868	0.0071	61.9	359.7	50317
		II	.107	.0131	7.6	81.5	6203
		III	.025	.0171	1.8	24.7	1449
	Sept.	I	.840	.0079	30.0	76.8	9734
		II	.130	.0138	4.6	20.8	1506
		III	.030	.0195	1.1	6.8	348
	Oct.	I	.784	.0084	24.4	15.1	1807
		II	.171	.0154	5.3	6.1	394
		III	.045	.0239	1.4	2.5	104
1968	May	I	.193	.0054	17.1	77.9	14303
		II	.726	.0109	64.4	584.2	53801
		III	.081	.0166	7.2	99.4	6003
	June	I	.268	.0059	46.6	153.0	26091
		II	.715	.0112	124.3	776.9	69609
		III	.017	.0175	3.0	28.9	1655
1968	July	I	.380	0.0065	40.9	154.7	23947
		II	.611	.0120	65.7	460.6	38504
		III	.009	.0186	1.0	10.5	567
	Aug.	I	.277	.0066	15.0	46.1	6982
		II	.685	.0120	37.1	206.8	17267
		III	.038	.0180	2.1	17.2	958
	Sept.	I	.161	.0056	9.4	4.2	761
		II	.814	.0108	47.5	41.6	3848
		III	.025	.0141	1.5	1.7	118
	Oct.	I	.164	.0062	10.1	.5	81
		II	.812	.0105	50.2	4.2	402
		III	.024	.0142	1.5	.2	12

[1] Catches of 0 age groups are not included.

TABLE 3.—Average weight in pounds by age. From aged catch landed in northern California and southern Oregon, 1955-1968.

Month	Age I	Age II	Age III
March	0.0038	0.0092	0.0146
April	.0043	.0098	.0152
May	.0049	.0104	.0158
June	.0055	.0110	.0164
July	.0060	.0116	.0168
August	.0060	.0121	.0174
September	.0065	.0127	.0180
October	.0070	.0132	.0185
November	.0074	.0135	.0190
January	.0086	.0140	

Fish and Game, personal communication) indicated that shrimp grow faster in the open season than during the closed season. Hence, the empirical curve was drawn to show seasonal differences in the growth rate. A more objective fit of the data could be obtained, but it would not alter the results enough to change the conclusions contained herein.

The curve shows relatively constant (linear) growth in weight during the open season, but slower growth during the closed period. The shrimp apparently do not approach an asymptotic weight prior to reaching maximum age in the fishery, and growth in weight could be described as linear during the exploited phase. Obviously, there was considerable variation, increasing with age.

Annual average count per pound for ages I, II, and III combined varied from 94 in 1961 to 142 in 1965 (Figure 4). Monthly values varied from 76 to 155 with an average for all years of 114.

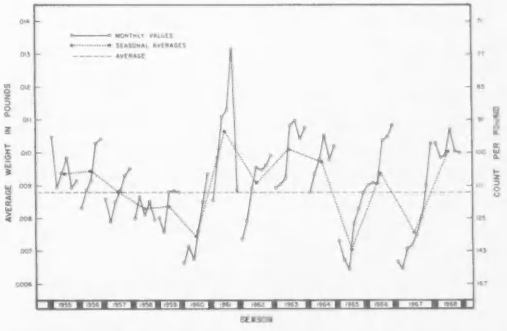

FIGURE 4.—Average size of ocean shrimp in the landings by month, season, and overall.

Because of the variation exhibited by the size at age data, it is possible that significant random or systematic errors are contained in the age composition data and that the subsequent analyses of these data will be correspondingly affected.

PARAMETER ESTIMATION WITH THE MURPHY METHOD

Reference Values

We used the generalized Murphy catch equation (Tomlinson, 1970) to analyze aged catch data. Gotshall (in press) provides estimates of natural mortality and biomass based upon a fishery independent randomized trawling scheme (Abramson, 1968). Since the biomass estimates are inherently negatively biased regardless of the catchability of shrimp and the mortality estimates may deviate from the population parameters in either direction, we decided to choose a natural mortality which would provide Murphy Method biomass estimates of a magnitude similar to those obtained from the randomized trawling scheme.

An annual natural mortality coefficient of $M = 1.44$ applied to all age groups yielded the appropriate biomass estimates. This is within the range of the M values given in Gotshall's (in press) Table 6 and cannot be considered significantly different from those estimates in view of the sizes of the standard errors shown in his Table 9.

Constructing Catch Ratios

Ratios of number caught in month $i+1$ to number caught in month i were calculated for all age III catches, giving values useful for within-season estimation of fishing mortality. To estimate across the closed seasons, the ratio of catch at age III in the first catch-month of season $i+1$ to catch at age II in the last catch-month of season i was calculated. For example, with 2 seasons and 3 months in each season, the ratios computed by this scheme would be: $R(1) = C_{III}(2)/C_{III}(1)$; $R(2) = C_{III}(3)/C_{III}(2)$; $R(3) = C_{III}(4)/C_{II}(3)$; $R(4) = C_{III}(5)/C_{III}(4)$; $R(5) = C_{III}(6)/C_{III}(5)$, where the catches used represent monthly catches by age (Table 4) and a closed season exists between months 3 and 4.

An additional assumption is that the exploitation rate (E) during the last month of each season is equal for ages II and III. Thus in the example, $E_{II}(3) = E_{III}(3)$. This assumption is necessary to allow estimation across the closed season.

Using these ratios for age III within season and age III to age II between seasons and assuming various exploitation rates for the last month of fishing in 1968, it was possible to make numerous estimates of the exploitation rates at age III during each month of fishing from 1955 to 1968. The Murphy method with backward calculation (Tomlinson, 1970) was used. The technique is similar to one used by Murphy (1965, 1966), except that Murphy used years instead of months, combined some age groups within years, had no years without catches, and did not treat year classes separately.

The data were separated into catches from year classes 1952 through 1967. Using the same hypothetical example as before (Table 4), the catch data can be put in the order $C_I(1)$, $C_I(2)$, $C_I(3)$, 0, $C_{II}(4)$, $C_{II}(5)$, $C_{II}(6)$, 0, $C_{III}(7)$, $C_{III}(8)$, $C_{III}(9)$. The catch ratios are computed as $C_I(2)/C_I(1)$, $C_I(3)/C_I(2)$, 0, $C_{II}(4)/C_I(3)$, $C_{II}(5)/C_{II}(4)$, $C_{II}(6)/C_{II}(5)$, 0, $C_{III}(7)/C_{II}(6)$, $C_{III}(8)/C_{III}(7)$, $C_{III}(9)/C_{III}(8)$. Since these catches all came from the same cohort, the Murphy method can be used to estimate $E_I(1)$, $E_I(2), \ldots, E_{III}(8)$, given that $E_{III}(9)$ is known. The previous analysis of age III data gave estimates of E at age III during the last month of fishing in each season, and these were used as starting values for backward calculation on each year class from 1952 through 1965. It was necessary in estimating E for the 1966 and 1967 year classes to choose values which gave an average population size in 1968 similar to the results obtained from fitting the Schaefer model.

Additional Modifications and Assumptions

Two additional assumptions fundamental to the results are: (1) ages II and III were exploited at the same rate, on the average, over the entire time period; (2) the catchability coefficient (q), computed as monthly catch-per-effort in weight divided by estimated average population weight for the combined age groups during the month, was reasonably constant over the entire time period. In order to satisfy these two assumptions, it was necessary to alter some

TABLE 4.—Hypothetical structure of age-structured shrimp catches and exploitation rates as arranged for analysis by the Murphy method.

Season	Catch-month	Catches by ages			Exploitation rates by ages		
		Age I	Age II	Age III	Age I	Age II	Age III
1	1	$C_I(1)$	$C_{II}(1)$	$C_{III}(1)$	$E_I(1)$	$E_{II}(1)$	$E_{III}(1)$
1	2	$C_I(2)$	$C_{II}(2)$	$C_{III}(2)$	$E_I(2)$	$E_{II}(2)$	$E_{III}(2)$
1	3	$C_I(3)$	$C_{II}(3)$	$C_{III}(3)$	$E_I(3)$	$E_{II}(3)$	$E_{III}(3)$
	Closed season						
2	4	$C_I(4)$	$C_{II}(4)$	$C_{III}(4)$	$E_I(4)$	$E_{II}(4)$	$E_{III}(4)$
2	5	$C_I(5)$	$C_{II}(5)$	$C_{III}(5)$	$E_I(5)$	$E_{II}(5)$	$E_{III}(5)$
2	6	$C_I(6)$	$C_{II}(6)$	$C_{III}(6)$	$E_I(6)$	$E_{II}(6)$	$E_{III}(6)$
	Closed season						
3	7	$C_I(7)$	$C_{II}(7)$	$C_{III}(7)$	$E_I(7)$	$E_{II}(7)$	$E_{III}(7)$
3	8	$C_I(8)$	$C_{II}(8)$	$C_{III}(8)$	$E_I(8)$	$E_{II}(8)$	$E_{III}(8)$
3	9	$C_I(9)$	$C_{II}(9)$	$C_{III}(9)$	$E_I(9)$	$E_{II}(9)$	$E_{III}(9)$

of the E values from the age III analysis used as starting values for the year class solutions.

An additional problem occurred which resulted in some final changes that were arbitrary and difficult to explain. For some years, especially 1955 through 1959, estimates of population size were quite low and q very high. It was demonstrated that a good transfer from age III to age II across the closed season did not occur for the year classes involved. Therefore, with year classes 1953 through 1958, 1962, 1963, and 1966, the estimation from the last catch-month at age II to the first catch-month at age I disregarded estimates during age III. It is hoped that the final result justifies these arbitrary decisions. It was also noted from the dots on Figure 3 that a growth curve from the sample data (Table 2) for seasons 1955 through 1959 indicates faster growth during the closed season than during the open season. This seems extremely doubtful in light of other contrary evidence and indicates that the problem was caused by inaccurate aging. Since age III shrimp make up such a small fraction of the catch and population biomass, it was not considered to seriously discredit final results.

Fishing Mortality Estimates

Estimation of monthly instantaneous fishing mortality coefficients, (F), was accomplished for each age group in each month by applying the Murphy method, as described above, to catches in numbers (Table 2). Since $M = 0.12$ was used as monthly instantaneous natural mortality for all months and ages, monthly exploitation rates, E, and monthly survival rates, s, may be obtained from

$$E = F\left[1 - e^{-(F+0.12)}\right]/(F + 0.12),$$

and

$$s = e^{-(F+0.12)}.$$

The estimates of F (Table 5) varied considerably, but age I was always exploited at a rate lower than ages II and III. During the 7 years, 1955-1961, average estimated F was 0.015 for age I, 0.056 for age II, and 0.057 for age III. In the 7 years, 1962-1968, $F(\text{I}) = 0.023$, $F(\text{II}) = 0.116$, and $F(\text{III}) = 0.159$. Averages for all 14 years were $F(\text{I}) = 0.019$, $F(\text{II}) = 0.088$, and $F(\text{III}) = 0.089$. Thus, as previously stated for a condition of estimation, ages II and III were exploited at about the same rates.

Converting fishing mortality to exploitation (Table 6), it was estimated that the fishery was removing about 5% of ages II and III and 1% of age I each month of fishing. Fishing intensity increased over the years and during 1962-1968 exploitation was nearly double that of 1955-1961 for each age. During the period 1961-1967, July and August were the most important months, followed by May, June, and September, while April and October were of little importance. Average F (Table 10) during these years, for

TABLE 5.—Monthly instantaneous fishing mortality coefficients.

Year	Month	Age group I	Age group II	Age group III
1955	May	0.001	0.011	0.006
	June	.003	.032	.013
	July	.004	.044	.011
	Aug.	.004	.055	.023
	Sept.	.007	.042	.021
	Oct.	.001	.002	.001
	Mean	.0033	.0310	.0125
1956	May	.003	.021	.042
	June	.002	.058	.046
	July	.002	.060	.029
	Aug.	.005	.112	.066
	Sept.	.003	.040	.020
	Mean	.0030	.0582	.0406
1957	May	.003	.022	.014
	June	.003	.009	.009
	July	.002	.005	.005
	Aug.	.038	.080	.096
	Sept.	.010	.026	.098
	Oct.	.002	.005	.020
	Mean	.0097	.0245	.0433
1958	May	.006	.039	.071
	June	.012	.081	.154
	July	.005	.030	.026
	Aug.	.020	.077	.068
	Sept.	.038	.060	.050
	Mean	.0162	.0574	.0738
1959	May	.016	.037	.090
	June	.042	.055	.053
	July	.036	.098	.113
	Aug.	.017	.038	.052
	Sept.	.043	.070	.120
	Mean	.0308	.0596	.0856
1960	May	.008	.030	.019
	June	.015	.038	.042
	July	.055	.080	.060
	Aug.	.052	.133	.168
	Sept.	.042	.109	.241
	Oct.	.010	.030	.040
	Mean	.0303	.0700	.0783
1961	June	.009	.048	.021
	July	.013	.077	.031
	Aug.	.020	.209	.137
	Sept.	.011	.098	.090
	Oct.	.005	.114	.059
	Nov.	.001	.005	.006
	Mean	.0098	.0918	.0590
1962	Apr.	.006	.034	.040
	May	.018	.099	.120
	June	.013	.016	.094
	July	.015	.122	.085
	Aug.	.045	.231	.193
	Sept.	.053	.354	.171
	Oct.	.022	.179	.200
	Mean	.0246	.1564	.1290
1963	Apr.	0.002	0.026	0.030
	May	.007	.105	.161
	June	.009	.140	.270
	July	.011	.204	.555
	Aug.	.029	.386	.762
	Sept.	.016	.267	.812
	Oct.	.007	.123	.100
	Mean	.0116	.1787	.3843
1964	May	.017	.071	.021
	June	.024	.119	.038
	July	.021	.080	.029
	Aug.	.055	.198	.072
	Sept.	.004	.015	.005
	Oct.	.008	.030	.010
	Mean	.0215	.0855	.0292
1965	May	.017	.069	.298
	June	.035	.128	.174
	July	.098	.137	.190
	Aug.	.037	.058	.098
	Sept.	.024	.036	.044
	Oct.	.013	.030	.040
	Mean	.0373	.0763	.1407
1966	May	.002	.057	.097
	June	.017	.262	.301
	July	.023	.423	.456
	Aug.	.009	.183	.140
	Sept.	.010	.142	.022
	Oct.	.006	.090	.030
	Mean	.0112	.1928	.1743
1967	Mar.	.001	.002	.030
	Apr.	.007	.011	.078
	May	.002	.003	.024
	June	.045	.100	.228
	July	.108	.180	.432
	Aug.	.063	.062	.325
	Sept.	.014	.018	.110
	Oct.	.003	.005	.040
	Mean	.0304	.0476	.1584
1968	May	.025	.098	.207
	June	.054	.162	.074
	July	.059	.116	.030
	Aug.	.020	.064	.060
	Sept.	.002	.017	.009
	Oct.	.001	.002	.001
	Mean	.0268	.0765	.0635

TABLE 6.—Monthly exploitation rates.

Year	Month	Age group I	Age group II	Age group III
1955	May	0.0004	0.0107	0.0056
	June	.0029	.0301	.0121
	July	.0041	.0408	.0103
	Aug.	.0040	.0505	.0218
	Sept.	.0069	.0387	.0194
	Oct.	.0003	.0019	.0009
1956	May	.0030	.0195	.0385
	June	.0024	.0531	.0422
	July	.0023	.0547	.0266
	Aug.	.0046	.0995	.0599
	Sept.	.0024	.0370	.0187
1957	May	.0031	.0203	.0134
	June	.0032	.0085	.0086
	July	.0017	.0045	.0046
	Aug.	.0349	.0720	.0860
	Sept.	.0091	.0241	.0883
	Oct.	.0017	.0047	.0187
1958	May	.0058	.0362	.0642
	June	.0114	.0736	.1346
	July	.0051	.0281	.0240
	Aug.	.0188	.0695	.0623
	Sept.	.0348	.0549	.0460
1959	May	.0146	.0346	.0812
	June	.0385	.0504	.0482
	July	.0332	.0881	.1011
	Aug.	.0160	.0356	.0482
	Sept.	.0396	.0638	.1067
1960	May	.0076	.0277	.0181
	June	.0141	.0350	.0387
	July	.0501	.0727	.0552
	Aug.	.0481	.1172	.1457
	Sept.	.0385	.0976	.2024
	Oct.	.0097	.0279	.0370
1961	June	.0083	.0442	.0290
	July	.0119	.0696	.0290
	Aug.	.0185	.1778	.1207
	Sept.	.0101	.0880	.0810
	Oct.	.0045	.1016	.0541
	Nov.	.0012	.0047	.0056
1962	Apr.	.0061	.0311	.0371
	May	.0171	.0885	.1064
	June	.0121	.0686	.0842
	July	.0140	.1084	.0767
	Aug.	.0416	.1946	.1657
	Sept.	.0483	.2820	.1485
	Oct.	.0208	.1550	.1712
1963	Apr.	0.0017	0.0246	0.0282
	May	.0067	.0943	.1402
	June	.0086	.1230	.2235
	July	.0104	.1744	.4037
	Aug.	.0267	.3028	.5062
	Sept.	.0147	.2211	.5282
	Oct.	.0064	.1090	.0898
1964	May	.0162	.0644	.0199
	June	.0223	.1054	.0347
	July	.0192	.0730	.0270
	Aug.	.0501	.1698	.0656
	Sept.	.0036	.0141	.0048
	Oct.	.0070	.0279	.0094
1965	May	.0162	.0629	.2433
	June	.0328	.1130	.1509
	July	.0880	.1206	.1635
	Aug.	.0346	.0528	.0878
	Sept.	.0222	.0338	.0407
	Oct.	.0119	.0279	.0370
1966	May	.0024	.0524	.0870
	June	.0160	.2179	.2458
	July	.0210	.3262	.3471
	Aug.	.0082	.1577	.1230
	Sept.	.0090	.1247	.0208
	Oct.	.0055	.0810	.0279
1967	Mar.	.0013	.0022	.0277
	Apr.	.0063	.0107	.0703
	May	.0017	.0029	.0219
	June	.0414	.0895	.1929
	July	.0968	.1554	.3323
	Aug.	.0573	.0569	.2622
	Sept.	.0133	.0166	.0983
	Oct.	.0028	.0050	.0370
1968	May	.0233	.0876	.1767
	June	.0492	.1409	.0676
	July	.0538	.1033	.0281
	Aug.	.0187	.0587	.0552
	Sept.	.0023	.0157	.0081
	Oct.	.0003	.0019	.0009

June to September, was 0.16 for age II, 0.21 for age III, and only 0.03 for age I.

Biomass Estimation

The Murphy method produces estimates of population size in numbers at the beginning of each catch interval. The present study also required estimates of biomass. Murphy (1966) stated he computed biomass by dividing the catch in weight by the appropriate estimate of E from his analysis of numbers in the catch. This would result in a positively biased biomass estimate, since it is equivalent to multiplying the number alive at the beginning of a catch interval by the average weight during the interval.

Two ways of computing the correct estimates of biomass utilizing Murphy's method to estimate numbers are possible:

(1) multiply the estimated average weight at the beginning of each interval by the number estimated for the population by the Murphy method. That is,

$\widehat{P^*_{ij}} = \hat{C}_{ij}\hat{w}^*_{ij}/\hat{E}_{ij}$ = estimated biomass to begin interval j, age i,

$\hat{w}^*_{ij}$ = estimated average weight for age i at beginning of interval j,

$\hat{C}_{ij}$ = estimated number of age i caught during interval j.

(2) Multiply the average number of age i alive during interval j by the average weight of age i individuals during this interval. That is,

$\hat{\hat{P}}_{ij} = \hat{\hat{N}}_{ij}\hat{\hat{w}}_{ij}$ = estimated average biomass of age i, during j.

$\hat{\hat{w}}_{ij}$ = average weight in the catch of age i, during interval j.

$\hat{\hat{N}}_{ij}$ = average number alive during interval j of age i.

For this study, the second method was used with average population numbers, $\hat{\hat{N}}_{ij}$, being given by

$$\hat{\hat{N}}_{ij} = \hat{N}_{ij}(1-e^{-t_j\hat{Z}_{ij}})/(t_j\hat{Z}_{ij})$$

$$\hat{N}_{ij} = \hat{C}_{ij}/\hat{E}_{ij},$$

t_j = fraction of year elapsed during interval j; $t_j = 1/12$ for all intervals.

$\hat{Z}_{ij}$ = total annual instantaneous mortality coefficient during j.

Total population biomass for ages I through III was computed as

$$\hat{\hat{P}}_j = \sum_{i=1}^{3} \hat{\hat{N}}_{ij}\hat{\hat{w}}_{ij}$$ = average biomass available during interval j, and the

catchability coefficient from

$$\hat{q}_j = \sum_{i=1}^{3} \hat{C}_{ij}\hat{\hat{w}}_{ij}/(\hat{\hat{P}}_j f_j)$$; f_j is effort expended during interval j.

Estimates of within-season monthly population biomass varied from a high of 12.0 million pounds in May 1955 to a low of 3.4 million pounds in October 1964 (Table 7). Population changes estimated by the Murphy method follow trends estimated by the Schaefer model (Figure 5), except Schaefer model estimates exhibit considerably less within season change. This difference in range of within season change was caused by the different ways in which the two models treat growth and recruitment. The Schaefer model assumes a continuous process for combined growth and recruitment, whereas the Murphy method treats growth as continuous (Figure 3) and recruitment as instantaneous (Table 7).

Estimates of monthly catchability (q) (Table 7) had extreme variation and showed an average within season increase (Figure 6). However, the within season changes were inconsistent and obscured by the variation. Monthly estimates of q varied from 21.3×10^{-5} in June 1968 to 3.8×10^{-5} in May 1955. Yearly averages had less variation and appeared to show no long-term trend (Figure 7). Average q over all months was about 9.0×10^{-5} which agreed closely with the value 8.5×10^{-5} used for the Schaefer model.

Spawning Biomass and Recruitment

Female spawning biomass consisted of all ages II and III shrimp plus some fraction of age I shrimp. Some data from commercial catch samples on the fraction of age I shrimp func-

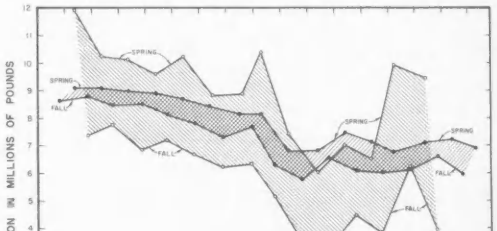

FIGURE 5.—Comparison of annual maximum and minimum population sizes as estimated by the Schaefer model and the Murphy method.

TABLE 7.—Ocean shrimp population biomass in thousands of pounds by age and month.

Year	Month	Ages I	Ages II	Ages III	Total	Est. $q \times 10^6$	Year	Month	Ages I	Ages II	Ages III	Total	Est. $q \times 10^6$
1955	May	9,100	2,670	265	12,035	38	1963	Apr.	4,101	3,000	358	7,459	84
	June	6,788	2,318	237	9,343	61		May	2,892	2,448	360	5,700	104
	July	7,119	2,051	208	9,378	91		June	2,830	2,008	227	5,065	95
	Aug.	6,538	1,731	181	8,450	89		July	3,546	1,772	134	5,452	81
	Sept.	6,467	1,481	157	8,105	51		Aug.	3,466	1,289	71	4,826	92
	Oct.	5,942	1,300	140	7,382	41		Sept.	2,979	785	27	3,791	120
1956	May	6,265	3,770	246	10,281	107		Oct.	2,939	609	10	3,558	132
	June	6,385	3,008	212	9,605	86	1964	May	3,790	1,970	317	6,077	83
	July	5,649	2,637	175	8,461	101		June	3,972	1,538	341	5,851	87
	Aug.	5,619	2,432	164	8,215	101		July	3,349	1,438	278	5,065	92
	Sept.	5,570	2,089	134	7,793	66		Aug.	3,363	1,177	222	4,762	123
1957	May	6,701	3,425	67	10,193	68		Sept.	2,542	908	183	3,633	145
	June	6,434	3,155	58	9,647	46		Oct.	2,378	810	167	3,355	148
	July	6,229	2,940	51	9,220	51	1965	May	5,676	1,281	176	7,133	49
	Aug.	6,067	2,625	42	8,734	95		June	4,764	1,147	134	6,045	75
	Sept.	5,405	2,207	34	7,646	82		July	4,657	942	105	5,704	80
	Oct.	4,872	1,975	29	6,876	118		Aug.	4,751	852	84	5,687	57
1958	May	6,710	2,811	129	9,650	58		Sept.	4,409	732	75	5,216	57
	June	6,739	2,501	108	9,348	80		Oct.	3,831	651	73	4,555	73
	July	5,704	2,096	84	7,884	62	1966	May	4,481	1,999	140	6,620	67
	Aug.	6,053	1,885	75	8,013	116		June	4,131	1,628	107	5,866	75
	Sept.	5,574	1,598	62	7,234	99		July	4,191	1,035	48	5,274	92
1959	May	6,650	3,372	256	10,278	113		Aug.	3,804	799	43	4,646	76
	June	6,441	2,922	222	9,585	93		Sept.	3,754	645	40	4,439	73
	July	5,895	2,459	176	8,530	92		Oct.	3,332	533	39	3,904	103
	Aug.	5,337	2,084	146	7,567	86	1967	Mar.	7,401	2,371	293	10,065	51
	Sept.	4,830	2,795	119	6,744	121		Apr.	6,853	2,246	274	9,373	57
1960	May	5,987	2,453	255	8,695	57		May	6,708	2,154	236	9,098	51
	June	6,217	2,419	276	8,912	62		June	6,566	1,895	174	8,635	70
	July	5,894	2,001	209	8,104	82		July	6,212	1,522	116	7,850	94
	Aug.	5,378	2,537	155	7,070	97		Aug.	5,741	1,309	76	7,126	80
	Sept.	5,048	1,343	117	6,508	100		Sept.	5,407	1,172	62	6,641	48
	Oct.	4,967	1,196	96	6,259	71		Oct.	5,049	1,148	62	6,259	51
1961	June	5,875	2,737	172	8,784	105	1968	May	3,105	5,991	480	9,476	95
	July	6,234	2,566	155	8,955	90		June	2,853	4,804	389	8,046	213
	Aug.	5,983	2,054	128	8,165	104		July	2,636	3,971	347	6,954	154
	Sept.	5,749	1,614	112	7,475	119		Aug.	2,295	3,219	286	5,800	100
	Oct.	4,885	1,391	110	6,386	145		Sept.	1,694	2,474	192	4,360	134
	Nov.	3,893	960	80	4,933	93		Oct.	1,667	2,116	170	3,953	155
1962	Apr.	6,888	2,956	601	10,445	59							
	May	6,714	2,631	518	9,863	73							
	June	6,197	2,424	500	9,121	66							
	July	5,764	2,076	404	8,244	63							
	Aug.	5,519	1,660	404	7,583	73							
	Sept.	5,358	1,095	232	6,685	106							
	Oct.	4,265	785	168	5,218	177							

tioning as females were made available from unpublished sources, but a good method for predicting the fraction of age I shrimp that would function as females was not found. Thus, a simple mean was computed from the data available for years 1957 through 1967 (Table 8). It is assumed that this mean proportion (0.33) predicts the fraction of the biomass of age I shrimp alive in September that will be females and that the sum of the September biomass of ages II and III, plus the fraction of age I functioning as females in September, is directly proportional to spawning biomass during the spawning season.

Recruitment was defined as the number of age I shrimp alive on May 1 of each year. Thus, the female biomass in September of season i is proportional to the biomass which will spawn sometime prior to May of season $i+1$ and the progeny of this spawning will be recruited to the fishery at the beginning of season $i+2$. Two

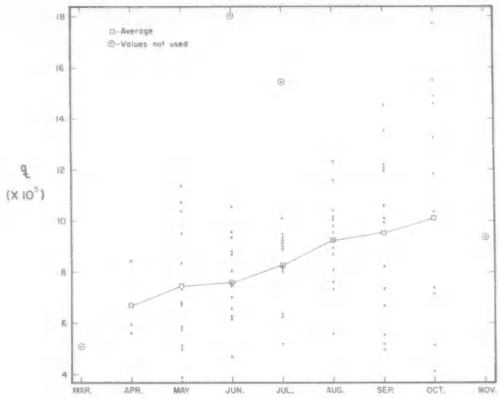

FIGURE 6.—Within-season changes in catchability coefficient (q). Line connects seasonal mean values. Circled points were not used to compute means.

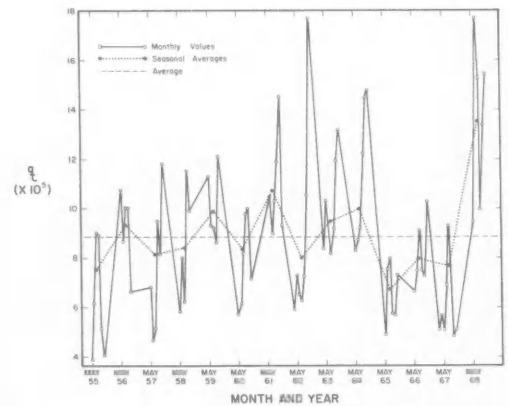

FIGURE 7.—Monthly catchability coefficients (q). Dashed line shows 1955-1968 mean.

TABLE 8.—Estimated percentage of numbers of shrimp functioning as spawners at age I.

Year	Percent	Year	Percent
1957	43	1963	21
1958	17	1964	36
1959	36	1965	51
1960	42	1966	24
1961	11	1967	54
1962	30	Mean	33

models for predicting recruitment from population biomass were tried.

$$\text{Model I}: \quad R_{i+2} = aS_i\, e^{-bS_i};$$

$$\text{Model II}: \quad R_{i+2} = cS_i\, e^{-dP_{i+1}}$$

where

R_{i+2} = number of age I shrimp on May 1, season $i+2$.

S_i = average biomass of functioning females during September of season i.

P_{i+1} = average total biomass (ages I, II, and III) during September of season $i+1$.

a, b, c, and d are constants.

Model I assumes the number of eggs produced is proportional to spawning biomass and that survival from egg to recruitment is influenced by this same spawning biomass. Model II assumes the number of eggs is proportional to spawning biomass and that survival from egg to recruit is a function of average biomass competing for the population space. September of season $i+1$ was selected for Model II because this seemed likely to be proportional to the average biomass encountered by age 0 shrimp, and data were available for all Septembers. May 1 was selected for recruitment since most seasons opened on this date.

Both models of recruitment were fitted by using transformations and a linear model (Paulik and Gales, 1965). The transformed equations are:

$$\text{Model I}: \log_e(R_{i+2}/S_i) = \log_e(a) - bS_i;$$

$$\text{Model II}: \log_e(R_{i+2}/S_i) = \log_e(c) - dP_{i+1}.$$

Estimates of recruitment by the Murphy method varied from a high of 1.5 billion shrimp on May 1, 1962, to a low of 0.6 billion on May 1, 1968. Spawning stocks producing recruitment varied from 4.5 million pounds in September 1959 to 1.8 million pounds in September 1963 (Table 9).

The range in recruitment observed at any given spawning stock size was very large relative to the range in size of spawning stock, and the fitting of Model I did not result in a meaningful

TABLE 9.—Recruits vs. spawners and population biomass.

Year (i)	[1]R_{i+2}	[2]S_i	[3]P_{i+1}
1955	1,341.6	3,772	7,793
1956	1,491.0	4,061	7,646
1957	1,295.8	4,025	7,234
1958	1,508.4	3,499	6,744
1959	[4]1,365.6	4,508	6,508
1960	1,502.0	3,126	7,475
1961	899.7	3,623	6,685
1962	685.3	3,095	3,791
1963	1,236.4	1,795	3,633
1964	947.1	1,930	5,216
1965	1,447.6	2,262	4,439
1966	613.9	1,924	6,641

[1] R_{i+2} = Recruits in millions on May 1 of year $i+2$.
[2] S_i = Spawners in thousands of pounds during September of year i.
[3] P_{i+1} = Population in thousands of pounds during September of year $i+1$.
[4] Estimated from June.

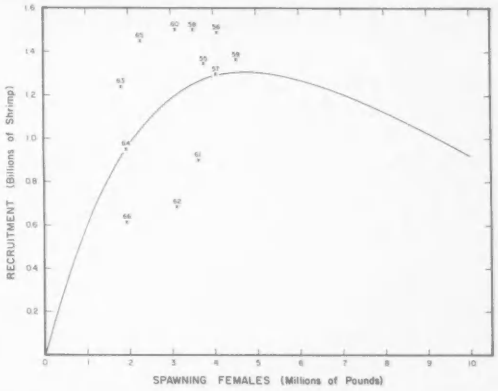

FIGURE 8.—Number of recruits on May 1 of year $i+2$ produced by spawning biomass of September, year i. Smooth curve represents Model I of the text.

relationship (Figure 8). Model II, which considers the effect of the population competing with the prerecruits, did not account for the variation in recruitment either. Consequently, a realistic spawner-recruit relationship could not be determined from the available data.

Yield per Recruit

Because a well-defined spawner-recruit relationship could not be determined the use of a self-generating model of the dynamic pool type, such as Walters (1969), is not feasible. We can, however, utilize the age-structured catch data to examine this type of model under the assumption that recruitment is constant.

We feel that the greatest confidence can be placed in the estimates of instantaneous fishing mortality (F_{ij}) for 1961 through 1967 (Table 5). For this reason, these values were combined to yield average monthly values ($\bar{F}_{ij}$). The averages were computed as simple arithmetic means to give vectors of average fishing mortality by month and age for April through October (Table 10), and allow for computations of yield per recruit. Yield per million recruits was computed by step-wise integration (Ricker, 1958; Paulik and Bayliff, 1967). For a season of l months, a year class would be exposed to fishing for $n = 3l$ months and protected for $3(12-l)$ months. This would give a total lifetime after recruitment of $L=36$ months. The yield can be expressed as

$$Y = \sum_{k=1}^{L} y_k = \sum_{i=1}^{3} \sum_{j=1}^{12} C_{ij}\bar{w}_{ij};\ k = 12(i-1)+j$$

where

$\bar{w}_{ij}$ = average weight taken from the empirical growth curve,
$C_{ij} = L_k E_{ij}$ = number caught in month j of year i,
$E_{ij} = \bar{F}_{ij}(1-e^{-Z_k})/Z_k$ = monthly exploitation rate in month j of year i
$Z_k = (\bar{F}_{ij} + M)$ = total monthly instantaneous mortality
(note that Z was previously used

TABLE 10.—Mean monthly instantaneous fishing mortality coefficients, $\bar{F}_{ij}$, by age group.

Month	Age group		
	I	II	III
April	0.005	0.024	0.049
May	.011	.067	.120
June	.022	.123	.162
July	.041	.175	.254
August	.037	.190	.247
September	.019	.133	.179
October	.009	.082	.068

to represent the annual mortality coefficient),

$L_k = R \exp\left[-\sum_{h=1}^{k-1} Z_h\right]$ = number survivors to begin interval k,

$Z_h = M$ during months closed to fishing.

R = number of recruits = 1,000,000.

M = 0.12.

The yields at various levels of fishing intensity were predicted by multiplying all $\bar{F}_{ij}$ by a constant equal to the intensity change desired and recalculating catches for all months. Estimates of expected yield in numbers and expected average weight per shrimp were also provided by this procedure. By setting appropriate values of $F = 0$, yields for various seasons and entry ages were computed.

If $M = 0.12$ is the monthly instantaneous mortality coefficient and if growth in weight at age is taken from the empirical growth curve (Table 3), a year class of shrimp that is not fished will reach its maximum biomass during the period July to August as age I. The biomass will then decline rapidly and by July to August as age II it will be about one-half the maximum.

The estimated yield per recruit for the period 1961 to 1967 was 0.00165 lb. per shrimp. Since the average annual catch during that 7-year period was 1.918 million pounds, it would have required an average of 1.162 billion recruits on April 1 to support the catch. The Murphy method estimates an average recruitment on May 1 of about 1.155 billion. Thus, the analysis of yield per recruit is in good agreement with the Murphy method results.

Given 1.155 billion recruits on April 1, it would require a yield per recruit of 0.00216 lb. per shrimp to obtain a total harvest approximately equal to the maximum sustainable yield estimated from the Schaefer model. To have obtained a yield-per-recruit of 0.00216 during those 7 years would have required an increase in fishing mortality of about 75% (Figure 9). This additional yield could not have been obtained by shortening the season or changing age at recruitment unless a substantial increase in fishing mortality accompanied the changes (Figures 9 and 10). With the distribution of fishing effort observed during 1961-1967, the average total monthly instantaneous fishing mortality ($\Sigma \Sigma F_{ij}$) operating against a year class during 3 seasons was estimated to be 2.0176. While maintaining total fishing mortality at 2.0176,

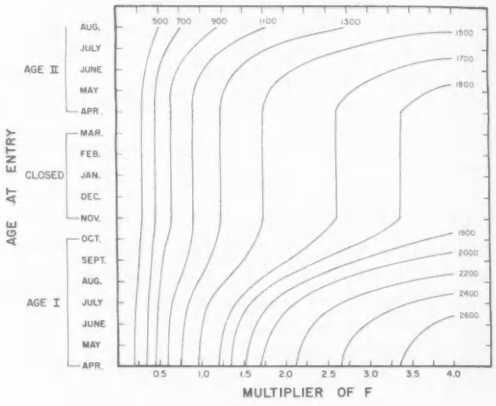

FIGURE 9.—Yield in pounds per million recruits as a function of age at entry into the fishery and fishing mortality. Fixed population parameters used were 1961-1967 means.

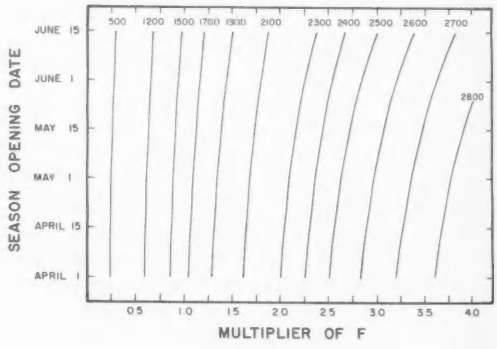

FIGURE 10.—Yield in pounds per million recruits as a function of season opening date and monthly fishing mortality coefficient. October 31 season closing date assumed and fixed population parameters used were 1961-1967 means.

the annual yield could theoretically be increased to about 2.8 million pounds by shifting fishing mortality so that I's and II's suffered equal rates. This would involve a 75% reduction in fishing mortality at ages II and III and assumes that the population with the new age structure would continue to produce 1.155 billion recruits. Such a change would also produce a reduction of 26% in the average size of shrimp in the catch and pose the problem of how the mortality pattern could be so altered.

INTER-MODEL COMPARISONS

Because we were unable to determine a spawner-recruit relationship and produce a self-generating form of the dynamic pool model, a realistic comparison of the results from the two types of models is not possible. In addition, the yield-per-recruit model treats natural mortality and growth parameters as constant while in the Schaefer model they are components of density dependent terms.

It is of interest to note that the biomass estimates obtained from the age-structured catch data by the Murphy method are in general agreement with the corresponding estimates of the Schaefer model. Although this does not compare the yield-per-recruit and Schaefer models, we feel it indicates some support of the Schaefer model from a semi-independent source. Another point of agreement between the yield-per-recruit and Schaefer models was that, given the average recruitment over the 1961-67 period, the former required a 75% increase in fishing mortality to produce the Schaefer model's maximum sustainable yield while the average annual effort expended during that period would require a 68% increase to reach the optimum effort level of the Schaefer model. However, as can be seen from Figure 9, maximum yield-per-recruit is predicted to occur at a much higher effort level under the previously mentioned assumption of constant parameters.

It seems clear from the foregoing discussion of results relative to the two models that management procedures should be based on the Schaefer model at the present time.

PROPOSED MANAGEMENT STRATEGY

Fitting an equation such as the Schaefer model to a set of actual catch and effort data may be viewed as merely an interesting exercise unless one has to make actual management recommendations based upon the results. Then the situation becomes somewhat sticky. It is obvious that a simple deterministic model such as Schaefer's will not precisely describe the dynamics of a fish population. At best, there will be fluctuations in recruitment, growth, and catchability which will cause some consternation to the manager attempting to use such a model.

In the case of the shrimp fishery, the management strategy we propose treats the Schaefer model estimates as exactly correct, responds to indicated deviations from the optimum population size in a relatively arbitrary but conservative manner, and integrates the Oregon and California fishing. This conservative strategy attempts a gradual reduction in the biomass when the model estimates it to be above P_{opt} and a rapid increase in the stock size when it is estimated to be below P_{opt}. To formulate this procedure, let Q be the catch quota (California + Oregon) and $C_e(P) = HP^2 - KP$ be the equilibrium yield obtainable from a population of size P. With $P(t)$ the population when the next fishing season commences,

$$Q = \frac{P(t) - P_{opt}}{2} + C_e\left(\frac{P(t) + P_{opt}}{2}\right);$$

$$P(t) > P_{opt},$$

$$Q = P(t) - P_{opt} + C_e\Big(P(t)\Big);$$

$$P(t) < P_{opt}.$$

When the model predicts the stock is in the surplus condition we are, then, proposing to harvest one-half of this surplus plus the predicted sustainable yield at the point midway between $P(t)$ and P_{opt}. A predicted stock deficit evokes a procedure which harvests the sustainable yield at $P(t)$ minus the amount by which the stock falls short of P_{opt}. For example, the 1970 California shrimp quota of 3.4 million pounds was set by the above method with $P(t) - P_{opt} =$

7.1 — 4.8 = 2.3 and C_e (5.9) = 2.3 for a recommended yield of 3.4 million pounds (Table 1). It was assumed the Oregon fleet's catch from Oregon waters would be negligible.

A more radical strategy such as harvesting all of the surplus stock could be employed, but the attendant risks would be higher. These risks would include a possible disturbance of whatever stability exists in the population, particularly with reference to age structure. It might also be argued that the observed catch-per-effort should be used to adjust $P(t)$ before making the quota calculation described above. Here again, a substantial risk would be involved if the observed catch-per-effort were much higher than the expected since with our methods it could not be determined whether such an anomaly was due to abnormal catchability or to a real increase in the stock size. The quota-setting procedure we recommended above does respond in a limited way to a higher than expected catch. Since the fishery operates under a quota, a catch-per-effort which is higher than expected will result in the quota being filled with a lower than expected amount of effort and usually in a shorter time period. An examination of (2) shows that this will increase $P(t)$ and thus result in a larger quota for the season beginning at time t.

This fishery must be carefully followed in the future to observe how well the model based upon current parameters describes the observed catch and effort pattern. An equation such as this which is fitted to data from only 16 years cannot be considered definitive from a statistical estimation viewpoint and, in addition, there is a chance the population parameters will actually be changing. For example, one cannot avoid speculating about the effect of the large Pacific coast hake fishery on the shrimp natural mortality rate. Since hake may be a substantial predator upon shrimp (Gotshall, 1969), a reduction of the hake population due to a large fishery might increase the abundance of ocean shrimp.

Beyond the technical management problems which we have discussed at length, there is the institutional problem of a single state attempting to manage an interstate fishery. While the catch from Oregon waters by Oregon-based vessels has usually been so small that it affects the population negligibly, at times it has been substantial. A sustained change in conditions could nullify the effect of California's quota mechanism.

ACKNOWLEDGMENTS

Many biologists of the Department of Fish and Game collected the data used in this paper. Daniel W. Gotshall and Walter A. Dahlstrom were of special help to us in obtaining the data and in freely passing on to us their knowledge of this shrimp fishery and of shrimp life history. We also wish to thank Catherine L. Berude for programming and computing assistance.

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OBSERVATIONS ON SCALE PATTERNS AND GROWTH OF THE PACIFIC SARDINE REARED IN THE LABORATORY

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ABSTRACT

Scale patterns and growth of Pacific sardine (*Sardinops caerulea*) were studied with laboratory-reared fish held for 24 months. All scales examined after the fourth month had accessory marks. The first accessory mark was formed in August to October and the second accessory mark, in May to August. The accessory marks were indistinguishable from annuli that formed in November to March.

Five possible causal factors of mark formation were investigated—temperature, salinity, gonad index, condition factor, and relative growth rate. Growth rate showed the best correlation. The accessory mark was formed during a period of change in growth rate and the annulus during a period of relatively constant growth rate.

An estimate of the body length-scale radius relation indicated that scales first increase in size at a body length of 33 mm.

Growth in length was rapid from the start of the experiment to the fourth month, after which the increase was gradual. The average instantaneous rate of growth was about 0.47/month during the first 4 months and about 0.03/month thereafter.

It was concluded that the abrupt increase in L_1 that was recorded in the 1940's for the sardine population was probably caused by errors in aging, owing to a change in scale readers and scale-reading criteria. The ages of fish age II and older were probably underestimated by the recent scale readers.

In the course of aging Pacific sardine (*Sardinops caerulea*) from scales, the senior author observed, from comparison of back-calculated lengths with growth curves, that accessory marks or false annuli occurred frequently and were easily mistaken for true annuli. This was contrary to the findings of Walford and Mosher (1943:8-9), who reported that the annulus was "present on all normal scales of an individual" whereas an accessory mark was only rarely present on "all the scales of an individual." Since misidentifying an accessory mark as an annulus can affect the estimated age of a fish, a laboratory experiment was conducted to determine (1) the frequency of occurrence of accessory marks, (2) the time of accessory mark formation, (3) possible factors that may cause accessory mark formation, (4) the time of annulus formation, and (5) the seasonal pattern of sardine growth. The experiment was initiated in May and was terminated approximately 24 months later. Results from the first 12 months of the experiment were reported by Kimura (1970), who showed that an accessory mark was present on scales of 4.5- to 5.0-month-old fish. This report is a more comprehensive presentation of results from the entire experiment.

METHODS

REARING

The collection of sardine eggs and the hatching and rearing of the young in the laboratory for the first 12 months were described by Kimura (1970). The general procedures, including those used after the 12th month, are briefly reviewed as follows. In May 1968, sardine larvae were hatched from eggs collected in plankton tows off San Diego, Calif., and the larvae were held in a

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polyethylene bag, which was suspended in a 4.6-m diameter pool (13.2 kliter). The pool also contained about 15 northern anchovy (*Engraulis mordax*) larvae. A 1,500-w mercury lamp that was suspended about 1 m above the bag provided illumination and a source of heat. The larvae were fed daily with plankton collected in Mission Bay, Calif., and live *Artemia*. On the 29th day the larvae were released into the pool. Feeding continued with plankton and live *Artemia* up to the 45th day, after which frozen *Artemia* and dry trout food were substituted. The daily ration was about 10% of the estimated total weight of fish alive on a given day, based on the average weight of fish sampled in the previous month.

On the 31st day the density of sardine larvae was noticeably reduced. Since few dead larvae were found during the previous days, the anchovies (average length 66 mm) were suspected of feeding on the sardines (average length 24 mm). Analysis of stomach contents of three anchovies revealed that they were indeed feeding on the sardines.[2]

During the first few months of the experiment, water was added to the pool only periodically to remove surface scum. But beginning on the 61st day, seawater was circulated continuously through the pool at an initial rate of about 19 liter/min. This rate was increased on the 180th day to about 34 liter/min.

SAMPLING

Fish were sampled and sacrificed at various intervals during most of the duration of the experiment. About 7-17 larvae were sampled daily from the polyethylene bag during the first month. During the second month 6-26 larvae were sampled primarily on a weekly basis. Starting with the third month and continuing through the 12th month, about 20-24 fish/month were sampled. After the 12th month, the sampling rate was reduced to 11-14 fish/month until an unusually large mortality from unknown causes reduced the population to 12 fish in the 16th month. Two more samples were taken thereafter; in one sample four fish were measured for length and returned to the pool. After the 24th month, the seven surviving fish were sampled and the experiment was terminated.

Standard length, total weight, gonad weight, and six scales removed from the body area at the tip of the pectoral fin (see Walford and Mosher, 1943:4) were obtained from most samples.

Water temperature was recorded daily on a thermograph. The monthly mean temperature ranged from 15.3° to 25.0°C and was generally 2.9°C higher than the monthly mean surface temperature recorded off the Scripps pier, La Jolla (Kimura, 1970), site of the water intake for the experimental pool[3] (see Lasker and Vlymen, 1969).

Salinity measurements were made by daily titrations from surface water sampled off Scripps pier. The mean values ranged from 33.09 to 34.38‰. It was assumed that water salinity was the same off the Scripps pier and in the experimental pool.

SCALE MEASUREMENTS

Scales were placed between two glass slides and viewed on a scale projector that magnified them 30 times. All marks that appeared to be annuli were recorded and the widths from focus to mark and focus to margin in the anterior field were measured.

ANALYSIS

Gonad weight was expressed as a percentage of total weight. This was designated a gonad index, or relative measure of sexual development.

The relative "fatness" of a fish was estimated

[2] To our knowledge there have not been previous reports on predation of sardine larvae by anchovies. The significance of our observation is that predation by anchovies may have contributed to the decline of the Pacific sardine population. Our anchovies were hatched from eggs and were 44 days older than the sardines. This difference in age (size) between the species is also found in the wild; the northern anchovy has a peak spawning period during January-March and the sardine, during April-June (Ahlstrom, 1966). The young of both species coexist in the California Current; thus it is conceivable that predation by anchovies is an important source of sardine natural mortality.

[3] The experimental pool was located at the Southwest Fisheries Center, about 1 km from the Scripps pier.

TABLE 1.—Results of aging of 205 known age, laboratory-reared sardines from scales.

Age (months)	Total number of fish	Total number of marks	Actual		Estimated				Percent disagreement
			Number with:		Number with:				
			0 mark	1 mark	0 mark	1 mark	2 marks	3 marks	
5	20	1	20	0	20	0	0	0	0
6	20	1	20	0	20	0	0	0	0
10	15	2	0	15	0	12	3	0	20.0
11	21	2	0	21	0	10	11	0	52.4
12	24	2	0	24	0	18	6	0	25.0
13	11	3	0	11	0	3	8	0	72.7
14	12	3	0	12	0	2	6	4	83.3
15	14	3	0	14	0	0	12	2	100.0
16	64	3	0	64	0	4	50	10	93.7
18	4	3	0	4	0	0	3	1	100.0

TABLE 2.—Frequency and percent (in parentheses) of Pacific sardines with various number of scale marks, as determined from scale reading. (Sardines were reared in the laboratory for 24 months.)

Age (months)	Number of fish	No mark	Accessory mark I	Annulus I	Accessory mark II	Annulus II
1	3	3 (100)				
2	8	8 (100)				
3	17	17 (100)				
4	9	4 (44)	5 (56)			
5	20		20 (100)			
6	20		20 (100)			
7	20		20 (100)	10 (50)		
8	20		20 (100)	13 (65)		
9	20		20 (100)	18 (90)		
10	20		20 (100)	20 (100)		
11	21		21 (100)	21 (100)		
12	24		24 (100)	24 (100)		
13	11		11 (100)	11 (100)	4 (40)	
14	12		12 (100)	12 (100)	6 (60)	
15	14		14 (100)	14 (100)	10 (100)	
16	64		64 (100)	64 (100)	64 (100)	
18	4		4 (100)	4 (100)	4 (100)	
24	7		7 (100)	7 (100)	7 (100)	7 (100)

by a condition factor (MacGregor, 1959). The factor (K) is calculated as a ratio of the weight in grams (W) to the cubic power of length in millimeters (L): $K = (W/L^3) \times 10^7$.

Back-calculated lengths from scale measurements were derived by two methods. Method one was by direct proportion, $L_m = (s_m/s_r)L$, where L_m = back-calculated length at time of mark (m) formation, s_m = scale width from focus to mark m, s_r = scale width from focus to margin, and L = length at sampling. Method two was also by direct proportion but with a correction factor (c) for body length when scales first increase in size in the Pacific sardine. The method uses the equation $L_m = c + (s_m/s_r)\ (L - c)$.

ACCESSORY MARKS AND ANNULI

FREQUENCY OF OCCURRENCE

An annulus is generally believed to form at annual intervals, usually as the result of a slowing down in growth such as occurs in winter for temperate species. An accessory mark, on the other hand, is believed to occur, if at all, at irregular intervals (Walford and Moser, 1943), the causes of which are unknown.

We examined the scales of the laboratory-reared fish and were unable to distinguish between the two types of marks. To test if other scale readers similarly could not distinguish accessory marks from annuli as we did, a series of scales from the laboratory-reared fish was mixed

with scales collected from wild fish and three experienced scale readers read the scales (Table 1). The percent error was as large as 100%, which indicates that accessory marks can indeed be easily misidentified as annuli.

TIME OF FORMATION

As many as four marks were observed on some scales. The percentage of fish with various numbers of marks was tabulated for each sample (Table 2). The results show that the first mark was formed from August to October (4-5 months old), the second from November to March (6-10 months old), the third from May to August (13-15 months old), and the fourth sometime after November (18 months old) but probably before January (20 months old). This January date for the fourth mark was deduced from two scales collected in late December from the bottom of the pool, but the data are not given in Table 2. The two scales had four distinct marks, but it is not known whether the scales were from one or two fish. The bottom of the pool was cleaned daily.

Based on the above criteria of an annulus and accessory mark, the second and fourth marks are annuli, and the first and third marks are accessory marks. The interval between annuli was about 12 months, and that between accessory marks was only 9 months.

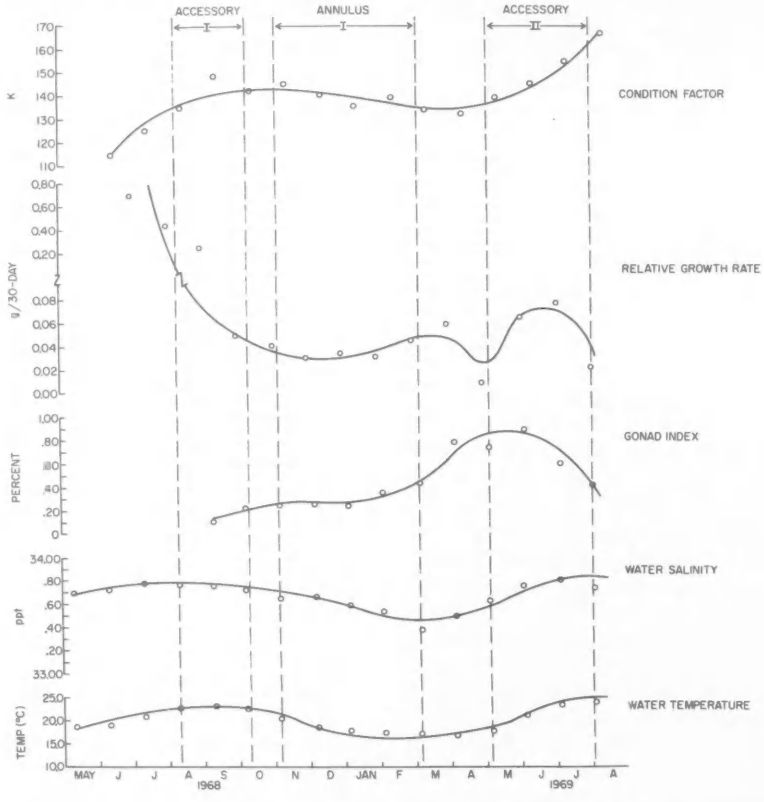

FIGURE 1.—Four possible factors that may be associated with mark formation on scales of Pacific sardines. Periods of mark formation are delineated by vertical lines.

POSSIBLE FACTORS AFFECTING MARK FORMATION

Water temperature and salinity, gonad index, condition factor, and growth rate were analyzed to determine whether they affected mark formation (Figure 1). Growth rate appeared to be best correlated with mark formation.

Kimura (1970) used monthly growth increments[4] for the first year to show that formation of the accessory mark was associated with maximum growth, and formation of the annulus was associated with the onset of rapid growth. His choice of growth increments for his analysis was not ideal because the magnitude of an increment is dependent on the size of the fish. We therefore chose to use the instantaneous rate of growth, $g = (\ln L_t - \ln L_0)/(t - t_0)$, Ricker (1958) on a 30-day basis to analyze the data from the entire experiment. The results (Figure 1) show that the accessory marks formed during periods of change in growth rate, whereas the annulus formed during a period of relatively constant growth rate.

GROWTH

BODY LENGTH-SCALE RADIUS RELATION

A body length-scale radius relation was fitted by least squares to data from 283 fish. A straight line of the form $Y = 32.856 + 9.030X$, where Y = standard length and X = scale radius, was calculated (Figure 2). The intercept of the line, or 32.856, is an estimated body length when scales first increase in size in the Pacific sardine. This estimate is probably too high, because scales with several circuli were observed on 26- to 30-mm long fish.

Landa (1953) reported 12 positive intercept values (68-191 mm) and 1 negative value (—102 mm) for body length-scale radius relations of fish caught by the commercial fishery in the 1940's. Compared to our estimate, his estimates are considerably larger. One reason for the difference is Landa used data from large fish (mean lengths of 186-228 mm), whereas we used data from small fish (mean length of 115 mm). This suggests that a relation over the entire size range of sardines may be nonlinear, although it is linear over a short segment of the curve. The parameters of a linear relation could hence vary, depending on the segment of the curve being examined.

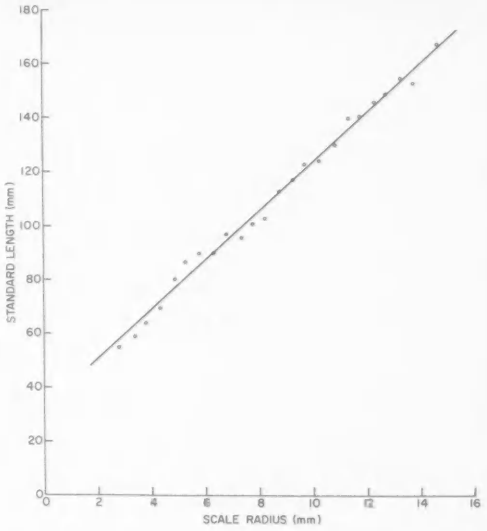

FIGURE 2.—Body length-scale radius relation for 283 laboratory-reared Pacific sardines.

WEIGHT-LENGTH RELATION

Data from 326 fish were used to estimate the weight-length relation. The relation (Figure 3) appears to underestimate the average weight of fish greater than 135 mm long. This is probably because the weight-length relation was based on data from individual fish whereas the data points in Figure 3 represent average weights for 5-mm groupings of lengths.

Clark (1928) estimated a weight-length relation for sardines landed at San Pedro, Calif., in the 1920's. Her estimate was compared to ours

[4] In Kimura's Figure 3 the notations for weight and length increments are mislabeled. The increments are not percentages but absolute values.

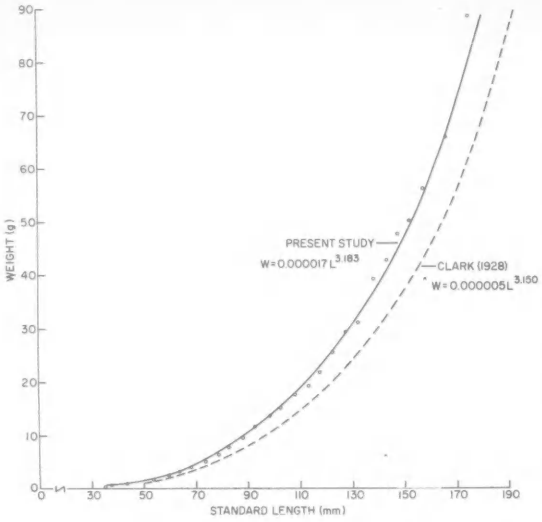

FIGURE 3.—Weight-length relation for the Pacific sardine.

(Figure 3) and found to be significantly different based on analysis of covariance ($F = 18.02$, df = 1, 237). The laboratory-reared fish were appreciably heavier for a given length than sardines caught in the 1920's. This may be attributed to several causes, among them difference in diet, in amount of exercise, and in the range of sizes sampled.

SEASONAL GROWTH PATTERN

Growth of the Pacific sardine has been well documented by several investigators (e.g., Walford and Mosher, 1943; Phillips, 1948; Felin, 1954; Clark and Marr, 1955). Most of the studies have concentrated on estimating growth based on scale readings of fish caught by the commercial fishery.

Another method of estimating growth is by rearing experiments. Although we recognize the limitation of laboratory vs. natural conditions, we believe that estimates of growth of laboratory-reared sardines can indicate the general trend in growth in the wild. We therefore estimated growth of our laboratory-reared sardines.

As shown in Figure 4, growth in length was rapid from the start of the experiment to the fourth month, after which the increase was more gradual. The average instantaneous rate of growth was about 0.47/month during the first 4 months and about 0.03/month during the fifth to 24th month. In contrast, growth in weight increased somewhat exponentially during two phases: during the first 4 months and again during the fifth to 14th month (Figure 5).

Walford and Mosher (1943) reported the standard lengths of juvenile sardines caught in monthly samples in the late 1930's. Although the date of birth, and hence the exact age, of

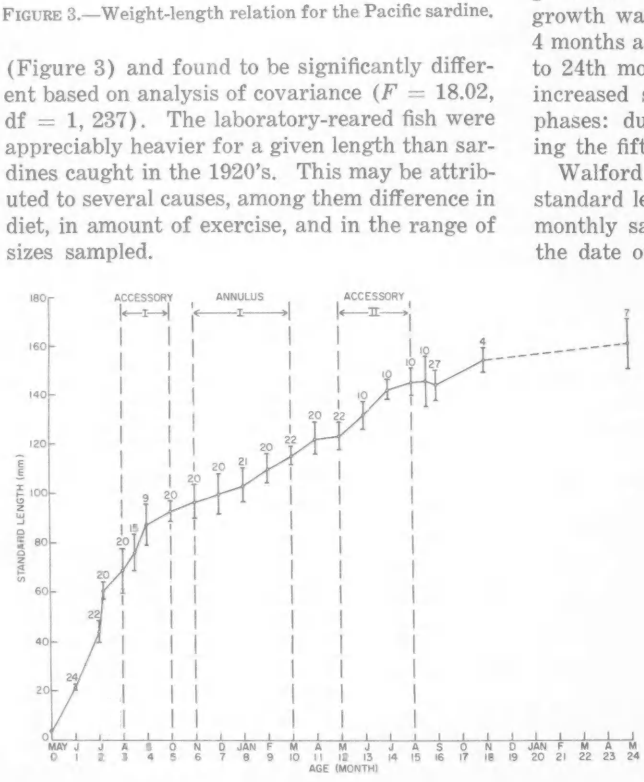
ACCESSORY I
ANNULUS I
ACCESSORY II
STANDARD LENGTH (mm)
AGE (MONTH)
MAY J J A S O N D JAN F M A M J J A S O N D JAN F M A M
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24

FIGURE 4.—Growth in length of Pacific sardines reared in the laboratory for 24 months. Mean length is represented by a circle, and one standard deviation is shown on each side of the mean. The sample size is also indicated. The first accessory mark occurred in August-October, and the second in May-August. The first annulus formed in November-March, and the second apparently in December.

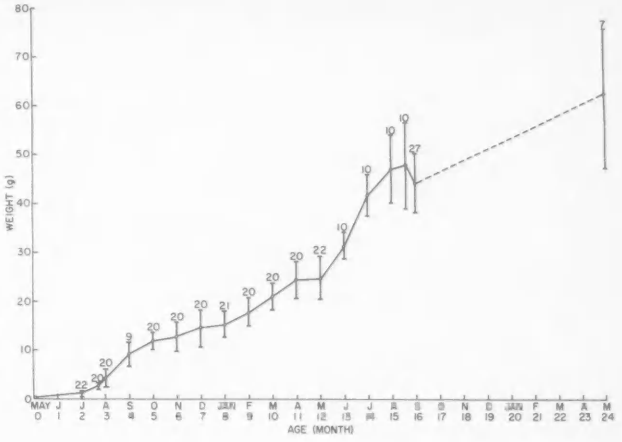

FIGURE 5.—Growth in weight of Pacific sardines reared in the laboratory for 24 months. Mean weight is represented by a circle, and one standard deviation is shown on each side of the mean. The sample size is also indicated.

their fish was not known, we compared their data for the 1937 and 1938 year classes with ours (Figure 6). The results indicate that although growth of the 1937 year class was fast, growth was similar in fish caught in the 1930's and in the laboratory-reared fish.

Marr (1960) presented data on the average length at time of first annulus formation (L_1) and showed that there was a sharp change in L_1 to a higher level with the 1944 year class landed at San Pedro. Using his data, we calculated separate estimates of average L_1: one for the 1934-43 year classes, and another for the 1944-57 year classes. The estimates are 101.3 and 131.5 mm, respectively. Compared with our estimate of 103.0 mm, growth of the 1934-43 year classes was almost identical to that for the laboratory fish, and growth for the 1944-57 year classes appears to have been faster than that for the laboratory fish. This faster growth may be an artifact and is discussed in a later section.

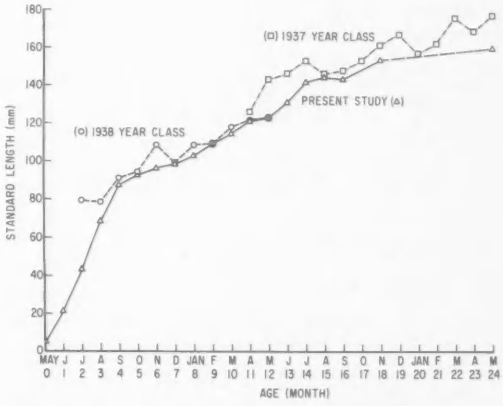

FIGURE 6.—Comparison of growth of juvenile sardines caught in the 1930's with growth of laboratory-reared sardines. Data for the 1937 and 1938 year classes are from Walford and Mosher (1943).

BACK-CALCULATED LENGTHS

Back-calculated lengths were computed for two samples, taken in September (16th month) and May (24th month). We reasoned that the back-calculated lengths would give an independent estimate of the time of mark formation, if growth is assumed to follow that shown in Figure 4. The average back-calculated lengths based on two methods are shown in Table 3. The first method gave lower estimates than the second. Both methods, however, gave back-calculated lengths that were reasonably similar to average lengths of samples collected during the period when the marks formed.

TABLE 3.—Back-calculated length of sardines sampled on two dates. The two methods of back-calculating length are discussed in detail in the text; in general, method 1 is by direct proportion, and method 2 is by direct proportion with a correction factor for the body length-scale radius relation.

Sampling date	Method	Average length (mm) at:					Sample size
		Accessory mark I	Annulus I	Accessory Mark II	Annulus II	Margin	
September	1	71.5	99.9	135.6	--	143.3	27
	2	88.9	110.6	137.8	--	143.3	27
May	1	75.1	104.7	137.4	153.1	160.3	7
	2	93.6	116.8	142.3	155.0	160.3	7

DISCUSSION

MARK FORMATION ON SCALES

Walford and Mosher (1943) indicated that on sardine scales an accessory mark was distinguishable from an annulus by its finer sculpturing and its rare occurrence on all scales of an individual. The results of our study on sardines reared in the laboratory showed that accessory marks occurred on all scales examined after the fourth month, and they were generally indistinguishable from annuli. But for some scales in which the accessory mark was distinguishable from an annulus, the identifiable characteristic was the fine sculpturing mentioned by Walford and Mosher.

Interruptions in the growth pattern are generally assumed to form marks on scales (e.g., see Van Oosten, 1957). It is also widely assumed that the driving mechanism behind mark formation is temperature, through the influence of a fish's metabolism (Brown, 1957). Our results indicate that mark formation is unrelated to temperature, but appears to be related to growth rate. Hogman (1968) obtained somewhat similar results in his experiments with coregonids. He found that formation of marks was closely related to growth and somewhat related to temperature. However, Hogman indicated that light period may be the primary driving mechanism. Bilton and Robins (1971) found that mark formation was correlated with increase in food supply, but not with resumption of feeding after starvation in sockeye salmon. Their experiments with light period proved inconclusive. It thus appears that mark formation in fishes is probably related to growth, although the actual driving mechanism(s) have so far not been clearly identified.

ERROR IN AGING

Scales are routinely used to age and study growth of the Pacific sardine. Our results indicate that extreme caution must be exercised in aging because of the presence of accessory marks on scales. Furthermore, since the annulus is formed during the winter, the actual age of a fish at time of first annulus formation may vary depending on its date of hatching. In our study the first annulus was laid down after the sixth month for fish hatched in May. May is the middle of the heavy spawning season for the Pacific sardine, but the season extends from March to October (Kramer and Smith, 1971).

Kimura (1970)[5] conducted an experiment to test the consistency of early and recent scale readers in aging sardines from scales. He found that the abrupt increase in L_1, as reportedly observed in the 1940's by Marr (1960) for sardines landed at San Pedro, may have actually been caused by a change in scale readers and in criteria used in reading scales. We compared our average length at annulus formation with the average L_1 of fish aged by the early ($L_1 = 101.3$ mm) and recent ($L_1 = 131.5$ mm) scale readers, and discovered that the early readers probably aged sardines correctly, whereas the recent readers probably underestimated the age of age II

[5] Kimura, M. 1970. Possible errors in locating the first scale annulus and in estimating the length of Pacific sardines. Manuscript filed at National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92037.

and older fish. If this was the case, and assuming that growth has not appreciably changed, then the number of fish that was incorrectly aged as age I by recent scale readers was at most equal to the number of fish correctly aged as age I. This is deduced from the fact that the presumably overestimated L_1 of 131.5 mm is about midway between our L_1 of 103 mm and L_2 (=length at time of second annulus formation) of about 160 mm.

Back-calculated lengths for Pacific sardines (Marr, 1960) have been based on Method 1. A statistical test of the intercept of our body length-scale radius relation (Figure 2) indicated that the intercept is not significantly different from zero (t = 1.831, df = 282). Although this indicates that Method 1 is acceptable, the back-calculated lengths at first annulus are appreciably and significantly different between Method 1 and Method 2 (Table 3). It is therefore advisable that Method 2 be used since it is the better procedure (Ricker, 1969).

We conclude from these results that a bias may be present in published accounts of the age composition of the Pacific sardine catch, which in turn may have affected studies on the population dynamics of the Pacific sardine. We recommend that the method of aging Pacific sardines be reevaluated, perhaps with the consideration of modifying the scale method so that the scale reader is made aware of the length of fish being aged or even utilizing other hard parts for aging, and that appropriate steps be taken to eliminate aging errors in the historic records on age composition of the catch. We realize that this task will not be easy, but it may be worthwhile because of the frequent use of the records to analyze fisheries hypotheses.

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UNSTRUCTURED MARINE FOOD WEBS AND "POLLUTANT ANALOGUES"

JOHN D. ISAACS[1]

ABSTRACT

The several species of fish living in the Gulf of California have been shown to possess quite different concentrations of cesium (and cesium in respect to potassium) than the same species of fish living in the Salton Sea. The Salton Sea fish display simple trophic steps of concentration, whereas those in the Gulf all show about the same levels. These differences are reasonably well explained by simplified trophic models of the two environments. The concentration factor found in the known and describable *food chain* of the Salton Sea, applied to a model of an assumed unstructured *food web* in the Gulf, leads to reasonable results. This suggests that study of the concentrations in marine organisms of such natural trace substances as cesium may lead to an understanding of the trophic position of the organisms, and hence constitute "pollutant analogues" that may yield a better understanding of the existing or potential distribution of pollutants in marine organisms.

Young (1970) found that the cesium content of the muscle of the several species of fish in the Salton Sea (California) increased by about a factor of 2 (average 2.15) in each of the successive steps in the simple linear food chain existing in that isolated marine environment and that the cesium/potassium (Cs/K) ratio similarly increased by about a factor of 3 (average 3.1). Results both for normal and radioactive cesium were in agreement. Young further demonstrated that the entry of the cesium into the food chain was via the phytoplankton, only. However, Young found that the same several species of fish in the Gulf of California displayed no such successive steps of increase, but rather, that the muscle tissue of all contained about the same concentration of cesium (with the supposedly more primary feeding mullets surprisingly having a somewhat greater than average concentration of cesium). Young's results are summarized in Table 1, where it can be seen that the Cs/K ratio is elevated by about a factor of 16 between the primary food and the fish in the Gulf of California.

Young suggested that these differences might be the result of a complex food web in the Gulf of California, and reported some evidence for this in the stomach contents of these Gulf fish.

DEVELOPMENT OF AN UNSTRUCTURED FOOD WEB MATRIX AND EQUATIONS

The following is an attempt to develop a highly simplified model of a generalized food web, to discuss some of its implications, and to test its validity by using real data.

Let us first assume that in a food web each transfer of organic material (or energy), or of individual elements such as cesium, from one component of the web to another can be characterized by the following quantities:

K_1 = a coefficient of conversion of matter (or energy) in food into living tissue

K_2 = a coefficient of conversion of matter (or energy) in food into irretrievable form (e.g., by respiratory combustion or mineralization)

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TABLE 1.—Summary of Young's results.

Item	Salton Sea			Gulf of California	
	Cs/K ratio × 10^6	Concentration factor relative to food		Cs/K ratio × 10^6	Concentration factor relative to food
Water	3.5 ± 0.1			0.823 ± 0.047	
Algae	4.0 ± 1.0			[1]0.823 ± 0.047	
Invertebrate[2]	3.8 ± 8.5	1.0 — 2.1			
Mullet	9.0 ± 1.1	2.3 ± 0.7	(algae)	15.2 ± 1.7	18.5 ± 2.0
Shad	14.8 ± 3.1	2.7 ± 0.7	(invertebr.)[2]		
Sargo-croaker	26.0 ± 2.7	5.5	(invertebr.)[2]	13.2 ± 1.0	16.0 ± 1.2
Corvina	57.7 ± 7.7	2.0 ± 0.3	(croaker)	10.4 ± 0.8	12.7 ± 1.0
	Average	3.1 ± 0.8		12.8 ± 1.1	15.6 ± 1.3

[1] Cs/K for algae taken as Cs/K for water.
[2] Concentration factor involves values for specific invertebrates within the range shown.

K_3 = a coefficient of conversion of matter (or energy) in food into nonliving but retrievable form (e.g., organic detritus or dissolved organic matter)

For each component

$$K_1 + K_2 + K_3 = 1 \qquad (1)$$

$0 < K_i < 1$, where $i = 1, 2,$ or 3.

These coefficients are assumed to apply to the nutrient processes of all heterotrophs in the system, microorganisms, invertebrates, and vertebrates alike. Further they are assumed to have constant mean values for each ingested component of a food web in which plant production is the only primary source.

Under these assumptions, some of the principal characteristics of a generalized food web can be represented by a matrix such as Figure 1. Each division along an abscissa represents the conversion of a fraction, K_1, of any arbitrary unit of food into living tissue. Therefore, the numbers on the horizontal axis are powers of K_1. Each division along an ordinate similarly represents the conversion of a fraction, K_3, of any arbitrary unit of food into retrievable but nonliving organic matter, and the numbers on the vertical axis are, thus, powers of K_3. These numbers can be used to name points in the matrix as in any set of cartesian coordinates. One use of the matrix can be illustrated by considering a unit of food, M_m, (e.g., in a copepod or in an edible nonliving particle) at 2, 3. If it is consumed by a heterotroph, the fraction K_1 is converted into tissue and the fraction K_3 into nonliving retrievable matter. The sum of these two fractions M_m $(K_1 + K_3)$ is now found at 3, 4. Its trajectory in the matrix is always to the right and down.[2] All points on a line at right angles to this trajectory (e.g., a diagonal line) can be considered to represent organic matter that has undergone the same number of steps of conversion from its origin as tissue of autotrophic organisms. The expression at the end of each diagonal line in Figure 1 is the sum of all fractions of an original unit of organic matter along that diagonal.

The number of possible paths from the origin to each point in the matrix is easily counted and is the sum of the two numbers of units shown at the point, the lower right-hand number being the number of paths resulting in living matter (or energy) at that point, and the upper left-hand number being the number of paths resulting in nonliving but recoverable matter (or energy) at the point.

It will be seen that this doubly infinite matrix is composed of two superimposed binomial (Pascal) triangles, and can be summed along diagonals resulting in two infinite series of binomials of the form:

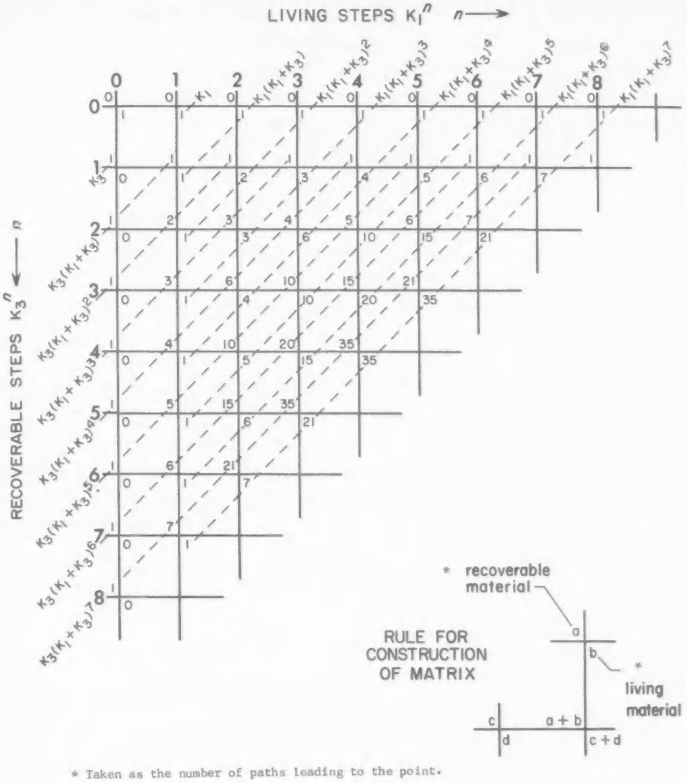
$$a + a(a + b) + a(a + b)^2 + a(a + b)^3 \ldots a(a + b)^n.$$

The sum of such a series is

$$\frac{a}{1-(a+b)} \qquad (2)$$

and for the sum of living matter (or energy),

[2] Cases may be considered in which either K_1 or $K_3 = 0$ and motion is either only to the right or only down. $K_1 = 0$ is, of course, not a permanently viable condition.



* Taken as the number of paths leading to the point.

FIGURE 1.—Matrix representing principal characteristics of a generalized food web.

$a = K_1$, $b = K_3$, and for the sum of recoverable matter (or energy), $a = K_3$, $b = K_1$.

These series can be further modified and summed in several ways. We will define a term, M_0, where M_0 is an increment of initial input periodically introduced into the system at intervals equal to the time taken by one average step in the food web. Under the assumption that all steps are equally probable, the diagonals along which the matrix has been summed mark equal intervals of time. Thus, allowing the quantity M_0 to be successively introduced at the origin of the matrix, the total quantity of material in the entire web, above the phytoplankton level, (M_t) for steady state becomes:

$$M_t = M_t' + M_t'' \tag{3}$$

where M_t' = total in living material, and

M_t'' = total in nonliving recoverable material;

$$M_t' = M_0 \frac{K_1}{1-(K_1+K_3)} = \frac{M_0 K_1}{K_2} \tag{4}$$

$$M_t'' = M_0 \frac{K_3}{1-(K_1+K_3)} = \frac{M_0 K_3}{K_2} \tag{5}$$

$$M_t = \frac{M_0(K_1+K_3)}{K_2} . \tag{6}$$

FURTHER VARIATIONS OF THE FOOD WEB MATRIX ANALYSIS

Later I will delete earlier steps in the matrix series. In this case, a more general solution of equation (4) involves a summation of the matrix above any step. Here the partial sum,

$$M_p' = \frac{M_0 K_1 (K_1 + K_3)^p}{1 - (K_1 + K_3)} \quad (7)$$

where p is the number of steps of the series eliminated.

Other types of formulations and summations are, of course, possible. For example, differences in the time for living-to-living and recoverable-to-living steps may be incorporated by multiplying the constant appropriate to the slower step by another constant representing the inverse ratio of the times of the two respective processes.

As another example, the average content of each *point* in time in the matrix can be derived by dividing each term of the series by the number of points along the particular diagonal.

Other manipulations of this matrix will be suggested later.

CALCULATION OF THE COEFFICIENTS OF THE PREDACEOUS FOOD WEB

For the purpose of examining Young's results on cesium, we will proceed with equations (4), (5), and (7) and test the hypothesis that the carnivorous fishes of the Gulf of California are members of an unstructured food web. That is to say that they randomly draw from the mean composition of the food web above the plant level.

Since, from the Salton Sea results, the Cs/K ratio increases by a factor of about 3 for each living step, we can say that

$$K_{1c} \cong 3K_{1f}, \text{ for organic food material} \quad (8)$$

and since the invertebrates in the Salton Sea which feed partially on detritus show no substantially different increase in Cs/K ratio, I will assume that a double step from living to recoverable to living material also results in an increase in the Cs/K ratio of only about 3, and, hence, that

$$K_{3c} \cong K_{3f} \quad (9)$$

where subscript c denotes the coefficients K_1 and K_3 applicable to the Cs/K ratio, and subscript f those applicable to food.

For the conditions in the Gulf of California, it is clear that, with the exception of the mullet, the fish do not consume plant material directly, and we can eliminate the first step in the series, and thus, for non-herbivorous omnivores, $p = 1$, and equation (7) becomes

$$M_p = M_0 \frac{K_1 (K_1 + K_3)}{1 - (K_1 + K_3)}. \quad (10)$$

Let us also define the Cs/K ratio in the plant material as:

$$q_c = \frac{M_{oc}}{M_{of}}$$

$$\text{then } \frac{M_{pc}}{M_{pf}} = \frac{q_c \dfrac{K_{1c}(K_{1c} + K_{3c})}{1 - (K_{1c} + K_{3c})}}{\dfrac{K_{1f}(K_{1f} + K_{3f})}{1 - (K_{1f} + K_{3f})}} = 16 q_c \quad (11)$$

where the coefficient 16 is approximately the mean increase in the Cs/K ratio from algae to predaceous fish in the Gulf (Table 1), and subscripts are as in equations (8) and (9).

Substituting (8) and (9), equation (11) *for food*[3] becomes

$$39K_1^2 + K_1(52K_3 - 7) - 13K_3(1 - K_3) = 0. \quad (12)$$

Assumption of a range of reasonable values of K_3 results in the following:

K_3	K_1	M_t'/M_0	M_t''/M_0	M_t'/M_t''
0.0	0.18	0.22	0.0	--
0.1	0.20	0.29	0.14	2.10
0.2	0.19	0.31	0.33	0.94
0.3	0.18	0.35	0.58	0.60
0.4	0.16	0.36	0.91	0.40

Values of ratios M_t'/M_0 (living material to input), M_t''/M_0 (recoverable to input) and M_t'/M_t'' (living to recoverable) are derived, but it is not known what values of these ratios might exist in nature.

The values of K_1, however, are within the range of values of conversion commonly found in laboratory experiments and culture operations involving growing animal populations.

We can thus conclude that the assumption of

[3] In the remainder of this paper, $K_1 \equiv K_{1f}$, and $K_3 \equiv K_{3f}$.

an unstructured food web in the Gulf of California in explanation of Young's findings on *predaceous* fish leads to reasonable estimates of the coefficient of conversion of food.

PELAGIC VERSUS SHALLOW WATER POPULATIONS

Other variations or testable conclusions or manipulations of these equations can be undertaken. For example, we can derive the relative biomass of two similar environments where, in one, the recoverable matter approaches zero. These might be a near-surface population over deep water where $K_3 \to 0$ because of rapid sinking of inert particles compared with a similar population over shallow water where K_3 could have any of the values shown in the table above.

From equation (4)

$$\frac{M_t' \text{ pelagic}}{M_t' \text{ shallow}} = \frac{M_0 \text{ pelagic}}{M_0 \text{ shallow}} \times \left(1 - \frac{K_3}{1-K_1}\right). \quad (13)$$

For the range of values found in the Gulf

$K_3 = 0.0$	$K_1 = 0.18$	$(1-\frac{K_3}{1-K_1})$	$= 1.00$
$K_3 = 0.1$	$K_1 = 0.20$	"	$= 0.88$
$K_3 = 0.2$	$K_1 = 0.19$	"	$= 0.75$
$K_3 = 0.3$	$K_1 = 0.18$	"	$= 0.62$
$K_3 = 0.4$	$K_1 = 0.16$	"	$= 0.52$

THE MULLET ANOMALY

The high Cs/K ratio of the mullet is difficult to explain. It is generally thought that the mullet is largely herbivorous. Three possible factors may give rise to the anomalous levels: First, the mullet in the Gulf of California may ingest far more organisms with the detrital material than is generally supposed, and these organisms may be part of a microscopic multistep food web that generates a high Cs/K ratio. No such effect was apparent in the Salton Sea, however, possibly because of the paucity and simplicity of invertebrate infauna in the detrital mat. Secondly, some members of the detrital community in the Gulf may take up inorganic cesium from the sediment, unlike those of the Salton Sea. Third, the high fat level of the mullet results in their possessing a caloric level, as related to organic material, that is 1.6 that of the other fish. This argues that it might be more significant to normalize cesium to calories than to dry organic weight, since more food intake (and hence more cesium) possibly is required for a given increment of growth in a fish with high fat content, with the potassium better normalized to fat free dry weight. This latter assumption would bring the Cs/K ratio in the mullet into the lower ranges of that in predaceous fish.

Pursuing this latter possibility, the adjusted Cs/K ratio for Gulf mullet can be set at about 10, and considering that the composition of the detrital feeding creatures (M_d) should be [from food represented by equation (5)]

$$M_d = M_0 \frac{K_1 K_3}{1-(K_1+K_3)}; \quad (14)$$

then the Cs/K ratio should be

$$\frac{M_{dc}}{M_{df}} = \frac{q_c \dfrac{K_{1c}K_{3c}}{1-(K_{1c}+K_{3c})}}{\dfrac{K_{1f}K_{3f}}{1-(K_{1f}+K_{3f})}} = 10q_c. \quad (15)$$

Substituting equations (8) and (9), as before, this becomes

$$K_3 = 1 - \frac{27}{7} K_1 \quad (16)$$

which is within the range of values for these constants previously derived (e.g., $K_3 = 0.30, K_1 = 0.18$). In simultaneous solutions of equations (12) and (16) values of K_3 are extremely sensitive to the values of concentration. The values of K_1, however, are essentially stable.

CONCENTRATION FACTORS

It should be noted in this discussion that the high concentration of cesium in the mullet may be a specific case of a more general principle, which is that the concentration factor (f_c) of a trace substance in a single step may be inversely

related to the coefficient of conversion of food (in terms of material). Certainly the upper value of f_c is limited to the total trace substance intake "diluted" by the new growth and hence,

$$f_c \not> \frac{1}{K_{1f}} \cdot \quad (17)^4$$

This argues that a creature with a low coefficient of conversion for food can show high concentrations of trace elements or pollutants for this reason alone.

Such lower coefficients of conversion and high concentration of trace elements may result from definitive growth, sickness or abnormality or, as probably in the case of the mullet, when food is converted into a more energetic form. Conclusions as to cause and effect of pollutant trace element concentrations in creatures with abnormalities must thus be considered with caution.

CONCLUSIONS

The assumption and analysis of an unstructured food web is reasonably consistent with findings on the concentration of the element cesium (in respect to potassium) in the Gulf of California. It suggests that unstructured marine food webs may be common and that the distribution of natural trace elements, such as cesium, may give insight into food webs in general, and hence into the existing or potential distribution of pollutants.

ADDENDUM

Several reviewers of this paper have suggested that I expand the treatment of trophic types in an unstructured food web. Dominance of any highly complex trophic types is incompatible with an unstructured food web hypothesis. However, the following may be considered compatible (from equations 4, 6, or 7 as appropriate):

Strict herbivores

$$M_n = M_0 K_1 \quad (19)$$

Omnivores

$$M_v = M_0 \frac{K_1}{1 - (K_1 + K_3)} \quad (20)$$

Particle feeders
(detritus + phytoplankton)

$$M_u = M_0 \frac{K_1 (1 - K_1)}{1 - (K_1 + K_3)} \quad (21)$$

Detrital feeders

$$M_d = M_0 \frac{K_1 K_3}{1 - (K_1 + K_3)} \quad (14)$$

Feeders on the detrital
milieu (detritus and detrital feeders)

$$M_{d+t} = M_0 \frac{K_1 K_3 (1 + K_1)}{1 - (K_1 + K_3)} \quad (22)$$

Strict predators

$$M_p = M_0 \frac{K_1^2}{1 - (K_1 + K_3)} \quad (23)^5$$

Non-herbivorous omnivores

$$M_v = M_0 \frac{K_1 (K_1 + K_3)}{1 - (K_1 + K_3)} \quad (10)$$

[4] This can be derived more formally as follows: let C_f be the concentration in the food; then

$$C_f = \frac{q_c}{q_f}$$

where q_c is quantity of the substance and q_f is total quantity of food material.
Then the concentration in the organism,

$$C_0 = \frac{q_c K_{1c}}{q_f K_{1f}} = C_f \times \frac{K_{1c}}{K_{1f}}$$

since

$$f_c = \frac{C_0}{C_f} = \frac{K_{1c}}{K_{1f}} \quad \text{, and}$$

$K_{1c} \not> 1$, then

$$f_c \not> \frac{1}{K_{1f}} \cdot$$

[5] Equation 23 could well have been employed instead of equation (10) in the previous treatment. Differences in results would be small, however.

These expressions can be employed to generate expressions for the coefficient R, or the increase in the concentration of any component passing through the food web and introduced only via plants. The derivation follows that of equation (11) above, where j is the coefficient of increase over the conversion of food, as in equation (8) above, where $j \cong 3$. Also, for interest, is shown the coefficient N, which is the limiting or maximum increase in the biomass of each trophic type resulting from a unit input into the food web (i.e. $M_0 = 1$), evaluated from the above equations.

	R	Equation No.	R^*	N^*
Strict herbivores	j	(24)	3.0	0.18
Omnivores	$\frac{jK_2}{1 - jK_1 - K_3}$	(25)	9.7	0.35
Particle feeders	$\frac{jK_2\,(1 - jK_1)}{(1 - K_1)\,(1 - jK_1 - K_3)}$	(26)	5.5	0.28
Detrital feeders	$\frac{jK_2}{1 - jK_1 - K_3}$	(27)	9.7	0.10
Feeders on the detrital milieu	$\frac{jK_2\,(1 + jK_1)}{(1 + K_1)\,(1 - jK_1 - K_3)}$	(28)	12.7	0.12
Strict predators	$\frac{j^2K_2}{1 - jK_1 - K_3}$	(29)	10.4	0.06
Non-herbivorous omnivores	$\frac{jK_2\,(jK_1 + K_3)}{(K_1 + K_3)\,(1 - jK_1 - K_3)}$	(30)	15.0	0.17

* for $K_1 = 0.18$, $K_3 = 0.30$, $j = 3$

It should be noted that the coefficient N indicates only the potential increase of the biomass of each trophic type, as related to productivity input. The potential population (standing crop) depends upon how closely this maximum is approached, and the fecundity, mortality, etc. of the appropriate organisms.

It should also be noted that the usefulness of the total assumptions of this model can be tested by the determination of R for an appropriate trace element, such as Cs, in samples of well defined trophic types.

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